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ECTOPARASITES OF MAMMALS

PROFESSOR VERNON LYMAN KELLOGG

STANFORD UNIVERSITY, CALIFORNIA

I

THE wingless permanent ectoparasites of mammals are chiefly of two groups, namely, the Mallophaga, or biting lice, which feed on the hair and dermal scales, and the Anoplura, or sucking lice, which feed on the blood. Certain mites and ticks, a few of the Pupipara (degenerate flies) and almost all of the fleas are also ectoparasites of the mammals, but the fleas, numerous and economically important as they may be, are not permanent parasites, for they live as larvæ not on the host of the adult, but in cracks and crevices in floors, or in the soil and elsewhere that the organic detritus used by them as food may be found. The adults, too, hop on and off their host, and often change from one host individual to another, and even from one host species to another. So that the problems of distribution and species-forming with which I am particularly concerned in my studies of the ectoparasites are not at all the same in such impermanent form as the fleas as in those truly permanent forms, the Mallophaga and Anoplura.

In these latter there occurs an extraordinary limitation of the parasite individuals and their immediate progeny and future generations to specific and even individual hosts (and *their* progeny and future generations), so that the Mallophagan and Anopluran fauna of any mammal usually represents a closely inbred family strain biologically iso-

lated from the rest of the individuals comprising the particular species represented by it. This brings about certain striking conditions of abundant small variation and subspecific (or intraspecific) distinction, which, however, because of the general similarity of habitat, food and habit, do not tend to grow rapidly into large (specific, generic, family) differences. The hundred or more species of Mallophaga so far recorded from mammals have, until very recently, all been ascribed to two genera, of which one included nearly nine tenths of the total number of kinds. There has been made a beginning—and not a particularly convincing one—at breaking up this inclusive genus (Trichodectes). It is a movement suggested more by the needs of convenience than the needs of expressing a biological situation. Similarly, although not representing so extreme a condition of likeness, the Anoplura, also including about a hundred parasite species (occurring only on mammals) have been, until recently, divided into but half a dozen genera, with the great majority of the species included in one. Certain aberrant forms found on man, the monkeys, the elephant, and on seals and walruses have always made necessary the recognition of four or five quite distinct genera. Attempts, however, are now being made to break up the unwieldly genus *Hæmatopinus*.

As this paper is, in effect, a continuation of my paper on "Distribution and Species-forming of Ecto-parasites" published in THE AMERICAN NATURALIST in March, 1913, which devoted itself to a consideration of the Mallophaga (some 1,400 species as so far known) found on birds, and to the problems presented by their conditions of life and their host and geographic distribution, I can dispense with any further account of the special biology of these parasites by referring the interested reader to this former paper. In it I have set out rather fully the special structural and habit features of the Mallophaga. Except that the Anoplura take blood, rather than feathers and hair, for food, and have specially modified

mouth parts to do it with, and are perhaps even more specialized in their physiological adaptations to their host than the biting lice, most of the general remarks made concerning the Mallophaga will apply to the sucking lice also.

In their peculiar special relations to their hosts as permanent ectoparasites on them, wingless, and reluctant to migrate even with opportunity, and so fitted physiologically to their parasitic life that they can not live for more than a few hours (or, at most, and exceptionally, days) off the bodies of their hosts, the Anoplura and Mallophaga are alike. And hence the conditions and problems of their distribution and species-forming are practically the same for the two groups.

The thesis that I have maintained, on a basis of the conditions presented by the bird-infesting Mallophaga, I now wish to test by the conditions presented by the mammal-infesting Mallophaga and Anoplura. This thesis is, in fewest words, that the host distribution of these wingless permanent ectoparasites is governed more by the genetic relationships of the hosts than by their geographic range, or by any other ecologic conditions. The fact, proved by abundant cases, that two host species of wholly distinct geographic range and with no possible opportunity for contact such as would permit of the migration of wingless parasites from one to the other, may have, nevertheless, one or more parasitic species common to them both, is associated almost always with the further fact that these common hosts are closely related genetically. They are most often of the same genus or of closely allied genera; they are almost certainly always of the same subfamily or family. The explanation for the possibility and the reality of this interesting host distribution I find in the hypothesis that the common parasite species has persisted unchanged from a common ancestor of the now divergent but allied host kinds.

Also, if it be true that genetic relationship is the deter-

mining factor in accounting for the host distribution of the parasites, then it is also true that the distribution of the parasites will indicate in some measure the genetic relationships of the hosts, and that occasional aid in determining the genetic affinities of birds and mammals of doubtful relationships may be had from a study of their parasitic fauna. In my paper already referred to I have pointed out some suggestive cases of this sort in connection with the birds and their parasites.

In examining the conditions existing among the mammals and their Mallophagan and Anopluran fauna, the first necessity was the compilation of a complete record or catalogue of mammalian hosts and their parasites, together with the record of the actual locality of each finding of parasites, together with a general record of the geographic range of all the various hosts. This catalogue, or set of records, I have now completed, and despite its meagerness compared with the similar catalogue of the bird hosts and their Mallophagan parasites from which the notes for the former paper were drawn, it contains enough records of interest to make worth while a preliminary report on the condition obtaining among the mammals and their parasites.

It is unfortunate that, although there are nearly one fourth as many mammal species as bird kinds, only about one hundred mammals figure in the Mallophagan host list, while Mallophagan parasites have been taken from over eleven hundred bird species. Also, only one hundred different Mallophaga have been taken from mammals, while about fourteen hundred have been taken from birds. Of the Anoplura, which are found only on mammals, records have been made from about one hundred host species, these records referring to just about the same number of Anopluran kinds. Thus the mammalian host catalogue with its list of parasites is a short one; as far as it goes, however, it is thoroughly interesting and suggestive.

In working up the records I have used Trouessart's

"Catalogus Mammalium" as an authority for the synonomy of the hosts, and my own judgment, based on a considerable personal knowledge of the parasites and on a careful consideration of all the more intelligible literature of the two groups, as a last court for the synonomy of the Mallophaga and Anoplura species. The synonomy of the parasites I have, however, not pushed far.

With so much of introduction and explanation we may come to a swift résumé of the results of a scrutiny of these records, proceeding by sequence of the mammalian orders, and referring to either or both groups of parasites as they may happen to be represented in the parasite records of the successive host groups.

II

The Marsupialia are represented in the host list by half a dozen species of kangaroos and wallabies (family Macropidæ) all from Australia, and a wombat, *Phascolomys ursinus* (family Phalangeridæ), from Tasmania (also S. Australia?). From all of these hosts only Mallophaga are recorded, no Anoplura having yet been taken from a marsupial. The six species of kangaroos represent three genera (Macropus, Petrogale and Æprymnus), and their Mallophaga are of seven species, representing four genera. Four of the species belong to the genus Boopia, and I strongly suspect are not all different. In addition there is one Trichodectes, from *Petrogale penicillata,* one Latumcephalum, from "wallabies," and one Heterodoxus, which is recorded from *Macropus giganteus* in Australia as well as from the same host in the Jardin des Plantes, Paris. It is also recorded from an undetermined wallaby in Victoria and one in Queensland, as well as appearing in three other records from "kangaroo" or "wallaby" from Australia. The parasite of the wombat is a species of Boopia, and it has been twice recorded from the same host. It is interesting that the kangaroo in the Jardin des Plantes harbored, even after some period of captivity, only its own proper para-

sites without accepting new ones from its many, various and closely pressing neighbors.

Of the four Mallophagan genera found on the kangaroo, three, namely, Boopia, Latumcephalum and Heterodoxus[1] are peculiar to them. The third genus, Trichodectes, is represented by but a single species which has been recorded but once. This is the common Mallophagan genus of mammals generally. The record is perhaps a good one, but its lack of confirmation by being unrepeated either for the same species or for any other species of Trichodectes, is suggestive. Heterodoxus, Latumcephalum and Boopia are two-clawed genera; that is, they are Mallophagan forms which belong to a family all the other genera of which are confined to birds. The characteristic structural difference between the mammal-infesting Mallophaga and the bird-infesting species is the presence in the first group of a single claw on each tarsus, and in the second of two claws. This difference is plainly an adaptive one concerned with the fitting of the foot for the seizing of hairs and scrambling about among them, on the one hand, and the manipulation of feathers and moving about on them, on the other. In examining living specimens under the microscope the special use and fitness of the feet, in the one case adapted to hairs and in the other to feathers, is obvious. However, Heterodoxus, Latumcephalum and Boopia, and, in addition, perhaps one other doubtful genus, represented by one species, and perhaps two or three species of another two-clawed genus, constitute exceptions to the general rule. It is of decided interest to note that the only genera of two-clawed Mallophaga found exclusively on mammals are limited to the Marsupials. The antiquity and isolation of

[1] The single valid species of this genus—the two or three that have been named are undoubtedly all the same—has also been recorded from dogs! In fact specimens in my own collection were received with the record "from Japanese dog." And Enderlein has recorded it from a dog from China and Neumann from a dog from Formosa. Yet dogs ordinarily do not harbor this parasite, and kangaroos and wallabies do. It seems necessary to believe that the dog host records indicate cases of straggling from kangaroos in zoological gardens or menageries.

this host group strongly suggests that the one-clawed condition common to all other mammal-infesting Mallophaga is a derivative from the original two-clawed condition characteristic of the parasites of birds and of these ancient mammals. The two-clawed condition is, of course, the one common to insects generally and is characteristic of the Atropids, in whom I am inclined to see the ancestors, or near-ancestors, of the Mallophaga. All of the Anoplura, it may be added, which are exclusively mammal-infesting, are one-clawed.

In this connection the suggestiveness of the fact that in face of the examination of many specimens of half a dozen species of kangaroos and wallabies, no Anoplura have yet been found on the Marsupials, may be referred to. I am coming strongly to believe that there is no such wide ordinal separation of the Mallophaga and Anoplura as our clinging to the fetich of "biting and sucking mouth-parts" as basis for radical classificatory separation has led us to effect. I believe, with Mjöberg, that the two groups of parasites have a fairly near genealogical affinity, their differences, which are particularly those of mouth-parts, being adaptive rather than palingenetic in character. The Anoplura have gone on from the Psocid-Mallophagan condition to a more specialized parasitic habit, and are the extremes of a general line of ectoparasitic evolution. The absence of sucking lice from the kangaroos may mean that the Marsupials are older than the Anoplura! No other considerable group of mammals, except certain families of strong-smelling Carnivora, is free from the blood-sucking parasites.

There are but two Edentates in the host list, one, the Cape Ant bear, *Orycteropus afer* (family Orycteropodidæ) of south and central Africa, harboring a sucking louse, of genus and species peculiar to it, and the other, the three-toed sloth, *Bradypus tridactylus* (family Bradypodidæ) of eastern South America, harboring a Mallophagan of species peculiar to it but of the genus *Gyropus* which is the less scattered, although still rather catholic,

genus of the two large ones characteristic of the mammals.

The large order Ungulata, with its numerous domesticated and semi-domesticated species, is a favorite host group with both Mallophaga and Anoplura. Altogether[2] about thirty Anoplura and two dozen Mallophagan species are recorded from fifty host species representing nine Ungulate families.

The family Elephantidæ is represented by the African and Indian elephants, recognized as distinct species of distinct geographic range. They both harbor a common Anopluran species, *Hæmatomyzus elephantis*, of species, genus and family peculiar to the elephants. Fahrenholz has given the varietal name *sumatranus* to specimens of these sucking lice taken from an Indian elephant in Sumatra. Records show that the parasites have been taken from their elephant hosts not only in Africa and Asia, but in various zoological gardens, as Paris, Hamburg and Rotterdam.

The small family of Hyracidæ, or conies, is represented in the host list by two species and perhaps a third one, one of which, the Syrian coney of west and south Asia, harbors one Anopluran and one Mallophagan, while from the other, the Cape coney of South Africa, the same Anopluran species is recorded as well as another of the same genus. This record of a second species is from a coney in the London Zoological Gardens. From the possible third species of Hyrax (taken in the African Congo and perhaps, but not probably, also a Cape coney), a second Mallophagan species is recorded of the same genus, Trichodectes, to which that of the Syrian coney belongs.

In the family Equidæ three species, the horse, the donkey and Burchell's zebra, all suffer from the infestation of a common Anopluran species, *Hæmatopinus asini*. In addition, the horse and the zebra have a common

[2] The synonomy in the parasite records, and indeed in the host records as well, is a vicious tangle. I have done the best I can, for the present.

Mallophagan parasite, *Trichodectes parumpilosus,* while the horse and donkey have another common biting louse, *Trichodectes pilosus.* Two varieties of *Trichodectes parumpilosus* have been named by Piaget, one from the zebra and another from "little horses of Java."

The pigs (family Suidæ), of which three wild African species besides the familiar animal of the barnyard are found in the host list, are infested by two (perhaps three) species of Anoplura and one (a not too certain record) Mallophagan. *Hæmatopinus suis* is found on the domestic *Sus* all over the world, while *Hæmatopinus latus* of Neumann, *H. phocochoeri* of Enderlein and *H. peristictus* of Kellogg and Paine, which are almost certainly all one species, are recorded from the wart hog, *Phacochœrus æthiopicus* from Nyasa-land, Africa, and probably also from another wart hog species from Africa, and the Red River hog, *Potamochœrus chœropotamus* from Nyasaland, Africa. In addition *Potamochœrus demunis* (probably), from German east Africa, is credited by Stobbe with a Mallophagan parasite peculiar to it, *Trichodectes vosseleri* Stobbe.

The peccary, *Dicotyles tajacu* (family Dicotylidæ) of Central America and southwestern North America, has a Mallophagan species peculiar to it, belonging to the smaller of the two large Mallophagan genera, namely, Gyropus.

The dromedary, of north Africa and western Asia, and the bactrian camel, of central Asia, harbor a common sucking louse, *Hæmatopinus cameli.* A doubtful second species called *H. tuberculatus* (Neumann thinks it identical with *cameli*) has been recorded from a dromedary imported from India into Australia. The "South American camel," the llama, harbors an Anopluran species peculiar to it, and two Mallophagan species, *Trichodectes breviceps* Rudow and *T. inæqualemaculatus* Piaget. Although Rudow's species are often suspect, I have just had his *breviceps* from a llama of Peru (collector C. H.

T. Townsend). With these llama Mallophaga there is also a small Anopluran which I have not yet worked out.

The family Cervidæ is represented in the host list by about ten species. They are infested by three species of Anoplura, each peculiar to its host, and six species of Trichodectes (Mallophaga) of which *T. tibialis* is common to the roe deer of Europe and Asia Minor, an African *Capreolus,* and our own black-tailed deer of the western states. *Trichodectes longicornis* is common to the red deer of Europe and Asia Minor and the fallow deer of south Europe, Asia Minor and north Africa.

The giraffe (family Giraffidæ) harbors a sucking louse, *Linognathus brevicornis,* peculiar to it.

The great family Bovidæ, with its many buffalo, buck, sheep, goat and antelope kinds, is represented in the host list by five or six species of Bos, four African bucks, three or four sheep, the ibex, chamois and two or three goats, and five or six antelopes, or gazelles. The domestic ox, *Bos taurus,* harbors three species of Anoplura and one Mallophagan. Curiously, none of these species is recorded from any other Bos. On the other hand, the zebu, the Indian buffalo, and the American bison all have the same Anopluran species (and no other, nor any Mallophagan), while the yak of central Asia and the Kaffir buffalo each have an Anopluran peculiar to it. The four species of African reedbucks and duikerboks have, according to the records, each a peculiar species of sucking louse. These records need scrutiny. One of them is my own, but I had to describe the species without seeing the types of the others. The domestic sheep carries two Anopluran species and one Mallophagan. The latter occurs also on at least two wild species of Ovis, one of west Africa and the other of north Africa. The fat-tailed sheep has a record from German southwest Africa of a Trichodectes of its own.

The domestic goat harbors one Anopluran and at least one Mallophagan, the latter being common also to the Angora goat, the chamois, and a wild (?) goat of Guinea,

and a wild (?) goat of Java. A recent description of a second Mallophagan species from the domestic goat is not convincing. The chamois has also an Anopluran, but one, so far, peculiar to it. Three species of Gazella (or Antilope) have three species of Trichodectes, of which one is common to two host species, one of Arabia and Syria and the other of north Africa and southwest Asia generally. This same Trichodectes is also recorded from the roan antelope, *Hippotragus equinus,* of east central and south Africa. One species of Gazella carries an Anopluran peculiar to it, as does also *Tragelaphus gratus* of west Africa.

The order Carnivora is represented in the host list by eight families and a total of fifty-four species. Only one species of Anopluran, the common sucking louse of the dog (not found yet even on the wolf or fox, both of which have other records) is recorded from a Carnivore, outside of the two families Trichechidæ (walruses) and Phocidæ (seals and sea-lions). From these two families, on the other hand, only Anoplura are recorded.

The family Felidæ is represented by three species, the domestic cat, the California lynx and the tiger. The cat and lynx have a common Mallophagan parasite, *Trichodectes subrostratus* (and no other), while the tiger has a biting louse presumably peculiar to it. The description of this parasite is, however, very brief and unsatisfactory.

The family Viverridæ, mongooses, ichneumons and genets, is represented in the host-list by eight species, of which five are of the genus Herpestes. Two of these Herpestes species, one of southern Spain, north Africa and Asia Minor, the other of west, east and south Africa, harbor a common Mallophagan parasite. A record of the finding of *Trichodectes subrostratus,* the familiar biting louse of the cat, on *Herpestes pluto,* comes from the Kameroons (Africa). It is probably a case of straggling, the mongooses being common enough in gardens, and some of them fairly domesticated.

Of the family Canidæ there are records from eleven

species, including the domestic dog, a wild dog of South America, two wild dogs of Asia, two foxes, and a wolf. The domestic dog has a familiar sucking louse and is also credited with that problematical normal or straggling biting louse of a peculiar genus which I have referred to in my account of the parasites of the kangaroos *Trichodectes latus,* the common biting louse of the domestic dog, is also common to the wolf, *Canis lupus,* of Europe and Asia, and to the raccoon-like wild dog, *Nyctereutes procyonoides,* of Asia and Japan. The record of this last came, it must be noted, from the Berlin Zoological Gardens. There is no other record of commonness of parasite to two hosts in the family. The English fox has a single Mallophagan species, and the California fox has another. The dhole, a wild dog of the Himalayas, has a Mallophagan species, and the Magellan wolf of Patagonia has another.

The family Procyonidæ is represented in the host-list by two raccoons, the California ring-tailed cat, and two coatis of Central and South America, respectively. The two raccoons, *Procyon lotor* of North America and *Procyon psora* of California, harbor a common Mallophagan parasite. In addition a German record (from a zoological garden?) credits *Procyon lotor* with carrying also a Mallophagan which is the characteristic parasite of the badger. On the California ring-tailed cat, *Bassariscus astuta,* have been found two Mallophagan species, one of which is the characteristic parasite of the skunks of North and South America. The two coatis, *Nasua narica* and *Nasua rufa,* one of southwestern United States, Mexico and Central America, and the other of South America from the equator south, both harbor a common Mallophagan species.

The family Mustelidæ, comprising the badgers, weasels, martens, and skunks, an ill-smelling crew, offers no attraction to blood-sucking parasites, but is represented in the host-list by nearly twenty species from which Mallophaga have been taken. The Old World badger has

a characteristic species, *Trichodectes crassus.* The martens, weasels and ermine have also a characteristic species, *Trichodectes retusus,* which is recorded from the pine marten of Europe and northern Asia, the beech marten of the same range, still another Old World marten, the weasel of Europe and Asia, the ermine of north Europe, Asia and America, and the weasel and mink of North America, in all six or seven species of Mustela and Putorius of very wide geographic range. The skunks of North and South America have also a characteristic Mallophagan species, *Trichodectes nephitidis,* described by Osborn from the common North American skunk. *Mephitis mephitica,* taken in Nebraska. I have found this parasite on the western skunk, *M. occidentalis,* in California, and on *M. macrura* of Arizona. It has also been recorded from the spotted skunk, *Spilogale interrupta,* of the southern United States, Mexico and Central America, and I have examples from a "skunk" of Bolivia. It is also recorded from a Chilian Mustelid, *Galictis quiqui,* which ranges over South America from the River Plate south, and from another species of Galictis in Brazil. Finally, examples of this ubiquitous pest are recorded from *Helictis everetti* from North Borneo! The last record comes from Neumann, a very careful and well-informed student of the parasites, but his specimens were taken from a skin in the Museum of Natural History of Paris. The Old World otter, *Lutra lutra,* has a *Trichodectes* of its own, as has also an African otter, *L. matschiei,* and the North African *Zorilla lybica.* Mjöberg records a species of Boopia (typical kangaroo parasite genus) from *Lutra pruneri* of India. As the record is an extraordinary one, being the only case of a Boopia found outside of Australia or on a mammal other than a Marsupial, it is well to note the exact circumstances of the record. The parasites (several examples) were got by Mjöberg from the Hamburg Zoological Museum where they were ticketed as having been taken from a "soeben frisch angekommenes Thier" of the species *Lutra pruneri,* the animal having been received

from India. There are to be considered in connection with this extraordinary record, first, the possibility of an exchange of labels in the course of the several handlings of the Mallophagan specimens, and, second, the possibility of a favorable answer to the question: Is *Lutra pruneri,* which does not appear in Trouessart at all, only *Lutra lutra,* the common Old World otter, and was the specimen from which the Mallophagan came a resident in a zoological garden in which kangaroos or wallabies also lived, affording a bare chance of straggling? The similar aberrant records from dogs of the kangaroo parasite *Heterodoxus* have already been referred to.

The bears (family Ursidæ) have, so far, but one parasite record to present, a Mallophagan species, *Trichodectes pinguis,* having been described from the Thibetan bear, *Ursus thibetanus,* a century ago.

The walrus (family Trichechidæ) harbors a strange Anopluran parasite of species, genus and family peculiar to its host, as, indeed, might be expected of any ectoparasite daring enough to brave comrade life with walruses. Examples of the parasite have been taken from walruses from Spitzbergen, Frobisher Bay (Davis Straits), the Hamburg Zoological Garden, and I have recently had them from a "Pacific walrus" from "southeast of Siberia."

The family Phocidæ is represented in the host-list by at least five species of seals and sea-lions carrying an equal number of Anopluran species representing three different genera, all of them peculiar to the seals. A single parasite species, *Echinopthirius phocæ* has been repeatedly taken from the fur seal, *Proca vitulina,* from both Old World and New World shores. The harp seal of the Arctic is credited with the same parasite, as well as another. Hooker's seal of New Zealand and the Auckland Islands carries an Anopluran, *Antarctopthirius macrochir,* of species and genus peculiar to it, while the elephant seal of the south Pacific has another parasite also of genus and species peculiar to it.

The large order Rodentia is well represented in the

host-list, representatives of thirteen families, summing about sixty species, being listed. Both Mallophaga and Anoplura infest the rodents, but certain families are parasitized almost or quite exclusively by Anoplura, while Mallophaga are the only parasites of others.

The Sciuridæ (squirrels and spermophiles), for example, with a dozen host species, are parasitized by a dozen species of Anoplura with only a single Mallophagan record; and a single record under such circumstances is always suspect. There is little commonness of parasite species to two or more host species in this family. Osborn's *Polyplax montana* is recorded from the eastern and western North American gray squirrels, and his *P. suturalis* has been taken from two Spermophile species, both, however, of the same general range. The well-differentiated parasite genus *Acanthopinus* is represented by one species from the common Old World squirrel, *Sciurus vulgaris,* and another from the eastern gray squirrel of North America. These species, though close together, really seem to be different. In addition I have just found the Acanthopinus species of the eastern gray squirrel on Douglas's squirrel in California, and another (new) species on a California chipmunk. The only Mallophagan species recorded from a Sciurid is *Gyropus turbinatus* from the marmot, *Arctomys marmotta,* of the mountains of southern Europe.

From the beaver (family Castoridæ) a characteristic Mallophagan species, *Trichodectes castoris,* has been taken in America. The beaver, it may be noted, is the host of the only beetle (*Platypsylla castoris*) that has become a specialized permanent ectoparasite, passing its whole life on the body of its host.

The Old World dormouse (family Gliridæ or Myoxidæ) harbors a sucking louse, *Polyplax pleurophœa.*

The large family Muridæ, including the rats, mice, voles and lemmings, is represented by twenty host species well scattered over the world. There are twenty-two Anopluran species and two Mallophagan species in the parasite list for the group. Both of these Mallophagan

records are my own. One is a new species of Colpocephalum (exclusively a bird-infesting genus) from a "spotted rat," Uganda, Africa, sent me by Sjoestedt in a collection made by the Swedish Zoological Expedition to Kilimandjaro-Meru, Africa, in 1905–1906. It is undoubtedly a straggler from some bird taken at the same time. The other is a poor specimen of Trichodectes from *Mus rattus,* Canal Zone, Panama, sent me by Dr. Jennings. It may be a good record—or it may be a deceiving one. Both record and specimen need further scrutiny. It is, perhaps, important to note that two specimens of a wingless Psocid (Atropidæ) were sent with the lot labeled "parasites from *Mus rattus.*" It would be very interesting if we could know that these Atropids were really living on the rats, feeding on their hair or dermal scales. I have found Atropids in rats' nests and birds' nests living undoubtedly on the loose hairs, feathers and dermal exuviæ. It is my belief, based primarily on certain striking facts of morphology, that the Mallophaga are degenerate descendants of the Rsocidæ.[3] Of the murid Anoplura, two or three are common to several hosts, as the well-known *Polyplax spinulosa,* recorded from all over the world from the now cosmopolitan *Mus rattus* and *Mus decumanus,* as well as from *Mus sylvaticus* of Europe and north Asia, and *Mus alexandrinus* of south Europe and Asia Minor (perhaps only a variety of *Mus rattus*), and *Polyplax affinis* (perhaps only a variety of *P. spinulosa*) recorded from *Mus agrarius* of eastern Europe, and *Mus sylvaticus* of Europe and north Asia. *Polyplax* (*Hoplopleura*) *acanthopus,* the common sucking louse of the mouse has been taken from the now cosmopolitan *Mus musculus,* and also from *Lemmus torquatus,* the lemming of Arctic Europe, Asia and America, *Microtus agrestis,* the field vole of Europe, *Microtus arvalis,* another common vole of Europe and Asia, and *Microtus* sp. from Iowa, U. S. A. The water rat, *Hydromys chrysogaster,* of Australia, has a Polyplax species of its own as has also *Otomys bisulcatus* of south and central

[3] See *Psyche,* Vol. 9, 339, pp. 1902.

Africa, *Hesperomys leucopus* of North America, *Epimys aurifer* of the Malay Peninsula, *Gerbellus indicus* of northern India and Afghanistan, and *Holochilus sciureus* of Brazil and Peru. The common Old World mouse, *Mus minutus,* harbors three Anopluran species, while *Mus musculus* has but two. The Old World water vole, *Microtus terrestris,* has a parasite differing from the two infesting respectively the two Old World land species of Microtus.

In connection with this résumé of the Murid parasites, I may say that I have now in process of working over some two hundred vials of material collected last summer from California mammals, which is going to add many records to the Murid list of both hosts and parasites. It will also add numerous records for the squirrels and spermophiles (Sciuridæ).

The family Geomyidæ, gophers, is represented in the host list by three North American and one Central American species. The Mallophagan species *Trichodectes geomydis* occurs on all of these hosts. The North American hosts are *Geomys bursarius* (Iowa), *Thomomys bottæ* (California), *Thomomys bulbivorous* (California), and the one Central American host is *Macrotomys heterodus* (Costa Rica). *T. bulbivorous* may be a synonym of *T. bottæ.* In addition, *Geomys bursarius* has yielded an Anopluran species of genus and species peculiar to it.

The pocket rats, family Heteromyidæ, are represented by a species of Perognathus (Baja California), and *Dipodomys merriami* (Arizona). From both are recorded the same Mallophagan species, *Trichodectes californicus.*

The jerboa, *Dipus* sp., is the sole representative of the family Dipodidæ. From it is recorded an Anopluran species taken in Tunis.

The Octodontidæ are represented by three species parasitized by one Anopluran and three different Mallophaga. The three hosts are of three different genera, one with an African range, the other two of South America. The parasite species on each is peculiar to it. A third

record, crediting the characteristic *Trichodectes pilosus* of the horse to a coypou of South America (in the menagerie of the Jardin des Plantes in Paris), is certainly either a false record or one of rather extraordinary straggling. The two Mallophagan species from these South American tuco-tucos belong to the genus *Gyropus,* which is the Mallophagan genus especially characteristic of the related South American families, the Caviidæ (guinea-pigs), the Dasyproctidæ (agoutis), and the Chinchillidæ (chinchillas and vizcachas) (see following paragraphs).

The guinea-pigs and mocos (family Caviidæ) are represented by three species, and are strongly parasitized by Mallophaga. They have no Anoplura. The domesticated form, which is variously held to be a species distinct from any wild one now known, or a variety of the wild species, *Cavia cutleri,* harbors two well-known species of Gyropus, namely *G. ovalis* and *G. gracilis* (this latter is held by some students to be of distinct genus). In addition, Piaget has described a species of Menopon (bird-infesting genus) from it, and Paine and I have described another Menopon from it from collections we have had from Peru and Panama. We have also found this latter species on the wild guinea-pig, *Cavia cutleri,* from Peru, and from this host Paine has described a species of Gyropus peculiar to this host. From the Brazilian moco, *Kerodon moco,* has been recorded a variety of *Gyropus gracilis,* one of the familiar species of the domestic guinea-pig, as well as another species of Gyropus peculiar to the moco. Recently Cummings has described a new Mallophagan taken at Villa Rica, Paraguay, from the wild guinea-pig, *Cavia aperea.* For this new species he established a new genus called Trimenopon. As a matter of fact the species is so much like Kellogg and Paine's *Menopon jenningsi,* except for its markedly larger size, that I am not at all sure it should be added as a fourth guinea-pig parasite.

A single agouti, *Dasyprocta aguti,* from Brazil, represents the family Dasyproctidæ. From it have been described two species of Gyropus peculiar to it.

The chinchillas and vizcachas (family Chinchillidæ, or Lagostomidæ) are represented in the host list by two species, to which I can add another (perhaps two others) on the basis of material recently received from Dr. C. H. T. Townsend, of Peru. From *Lagidium peruanum* Gay long ago described a peculiar Gyropus, and I have specimens of a Gyropus which may or may not be different from Gay's species. His description is very meager. In addition I am about to describe, under the name *Philandria townsendi,* another species, representing also a new genus, specimens of which have been sent me by Dr. Townsend from the same host. Also in this Townsend sending are specimens of a small Polyplax species (Anopluran) from the same host.

The Cercolabidæ or Coendidæ, American porcupines, are represented in the host lists by five species, three of Central and South America and two of North America. They harbor no Anoplura, but are parasitized by two Mallophagan species, of which one, *Trichodectes setosus,* occurs on all the host species in the list. The second Mallophagan is a *Trichodectes* recently described by Stobbe from *Cercolabes nova-hispaniæ* of Mexico and Central America. The other South American host porcupines are *Coendu* (*Cercolabes*) *prehensilis* (northern South America) and *C. villosus* (Brazil). The North American hosts are *Erethizon epixanthum* (California) and *E. dorsatum* (Nebraska).

Finally the family Leporidæ, hares and rabbits, appears in the host list with six (perhaps only five) representatives, of which four, namely, *Lepus timidus,* of circumpolar arctic regions, *Lepus cuniculus,* native to Europe and north Africa but introduced over the whole world, *Lepus europæus* of Europe and *Lepus campestris* of western Canada and United States, harbor the same species of sucking louse, representing a genus peculiar to hares and rabbits. I must note that this species, *Hæmatopinus ventricosus* Denny, is commonly referred to as two species, of which one, *H. ventricosus,* is recorded from the American host species and *L. cuniculus,* while

the other, called *H. lyriocephalus,* is recorded from *L. timidus* and *L. europæus.* But Neumann, an exceptionally experienced student of the Anoplura, holds that the two species are one. A deer-infesting Mallophagan, *Trichodectes tibialis,* certainly a straggler, has been recorded from *Lepus europæus,* and another Trichodectes (a very old and uncertain record) from *Lepus cannabinus.*

The order Insectivora is represented by but two species, the mole, *Scalops argentatus,* of North America, and the shrew, *Sorex araneus* of Europe and Asia. Each harbors an Anopluran species, that of the mole being a curiously modified form and of species and genus peculiar to its host, while that of the shrew is of a species not found on other hosts.

The order Prosimiæ, the lemurs, presents a single record, that of a species of Mallophagan, *Trichodectes mjöbergi* Stobbe, described from the North Bornean *Nycticebus borneanus* (family Nycticebidæ).

The order Primates is represented in the host list by four families, the Cebidæ of the New World, the Cercopithecidæ, the single family of apes, Simiidæ, of the Old World, and the family of man, Hominidæ. The distribution of the ectoparasites of these groups is of unusual interest to the special student and will likely prove equally so to more general students.

The Cebidæ, platyrrhine, tailed, New World monkeys, are represented by two species, the spider monkey and one of the howling monkeys of Brazil, members of different genera, each with a Trichodectes species peculiar to it. In addition three species of Ateles, one of Mexico and Central America, another of Guiana and Brazil, and the third an undetermined species of the genus represented by a specimen in a traveling menagerie in Europe, have yielded three species of the Anopluran genus Pediculus, otherwise characteristic of man and the anthropoid apes. These three Pediculus species have been recorded and described by three different students of the group, all careful workers, and there can be no doubt of the generic reference. But it is to be noted that the specimens of all three

parasite species were obtained either from host skins in a museum (in one case the Zoological Museum of Hamburg, in another, the Berlin Museum) or from a live host in a menagerie. In no case, therefore, is the possibility of a straggling record wholly excluded, but the coincidence of three discoveries makes the records practically safe. Finally, in this connection it is to be noted (as I have already pointed out in a brief paper[4]), that, although Ateles is a tailed New World genus and presumably widely separated genetically from the anthropoids, Friedenthal has affirmed, on a basis of blood and hair comparison, that Ateles shows unmistakable differences from other tailed monkeys, and resemblances with the anthropoids, and he suggests that in Ateles we should see monkeys, which, in a certain sense, replace, in the New World, the anthropoids of the Old. It is, in any event, a strange thing that Ateles differs from the other Cebidæ and from the Cercopithecidæ as well, in not harboring the Anopluran genus Pedecinus to which all monkey-infesting Anoplura, except those of the simians, belong, but in actually harboring parasite species of the genus found elsewhere only on the simians and man.

The family Cercopithecidæ, catarrhine, Old World monkeys, is represented in the host list by a dozen species, from which one Mallophagan species, viz., my *Trichodectes colobi* from a guereza monkey, *Colobus guereza* var. *caudatus* (East Africa), and ten Anopluran species have been recorded. Of the Anoplura nine species belong to the genus *Pedecinus,* long recognized as the characteristic genus of the lower monkeys, as contrasted with the genus *Pediculus* characteristic of the anthropoid apes and man. For the tenth species, Fahrenholz establishes the new genus *Pthirpedecinus,* just as for one of the man-infesting species the separate genus *Phthirius* had to be established. There are several cases of the commonness of a single Pedecinus species to two or three hosts. *P. breviceps* Piaget is recorded from *Macacus silenus* of

[4] "Ectoparasites of the Monkeys, Apes and Man," *Science,* N. S., Vol. 38, pp. 601–602, 1913.

India, *Cercopithecus mona* of west Africa, and a third *Cercopithecus* skin in the Zoological Museum at Hamburg. *P. longiceps* Piaget is recorded from *Macacus cyclopis* of Formosa, *Semnopithecus maurus* var. *cristatus* of Borneo, and *Macacus cynomolgus* of the Malaysian region. *P. eurygaster* Gervais has been recorded from *Macacus sinicus* of India and on a macaque in the Zoological Garden at Sydney, and another in the Zoological Garden at Melbourne. A hamadryad (Paphio sp.) of north Africa has a Pedecinus species peculiar to it, as has a *trachypithecus,* of Malaysia, and the Barbary ape, *Macacus innuus,* of northern Africa and Gibraltar. The common *Macacus rhesus* carries one species of Pedecinus peculiar to it, and that single species of Phthirpedecinus already referred to. *Macacus silenus* also has recorded from it two species both belonging to *Pedecinus.*

The family Simiidæ, anthropoid apes, is represented in the host list by three species, namely, the chimpanzee and two gibbons. One of these gibbons is *Hylobates syndactylus* of Sumatra; the other is *H. leuciscus* of Borneo. A single species of *Pediculus* is common to them both, and is not elsewhere recorded. The chimpanzee has also a single species of *Pediculus* which is peculiar to it. No Pedecinus has been taken from a Simian.

Finally man, representing the fourth Primate family, Hominidæ, is the host of three notorious Anopluran species, two of which are species of Pediculus and the third the only species so far known of another genus, Pthirius. Neumann is inclined to see in *Pediculus corporis* only a variety of *Pediculus capitis.* All of these parasites are found on man in all parts of the world. Some curious variations among the parasite individuals are shown, perhaps the most curious being a plain tendency to a darker coloration of the individuals occurring on the bodies of men of the dark-skinned races. In my brief discussion elsewhere, already referred to, I have noted the interesting significance of this possession by man and the anthropoid apes of a common genus of Anopluran parasites, while the parasites of the lower monkeys belong to

a well-distinguished other genus. There is no doubt that the close physiological fitting of parasites to host makes their host distribution significant of genetic or "blood" relationship, and this commonness of one type of parasite to man and the apes, and its limitation to these hosts, and replacement on the lower monkeys by another parasitic type, is an added indication of the actual blood-likeness of the Simians and man, a likeness apparently greater than that between the Simians and the lower monkeys.

III

In the light of the plain statement in part I of this paper of my belief gained from a study of the distribution of the bird-infesting Mallophaga, to the effect that the host distribution of the permanent wingless ectoparasites of birds is determined more by the genetic relationships of these hosts than by geographic relationships or any ecological condition, and the corollary of this, which is that the distribution of the parasites may therefore often have a valuable significance as to the genetic relationships of animals whose genealogic affinities are in process of ascertainment, and in the light of the facts of distribution for the mammal-infesting Mallophaga and Anoplura as just set out in part II of this paper, I hardly need to do more, in conclusion, than to point out that the distribution conditions exhibited by the mammal parasites, even in the face of the meager knowledge that we yet have of the mammal-infesting forms, clearly, on the whole, confirm this thesis. In fact, considering how few mammal-infesting parasite species we yet know, it is surprising how repeatedly the commonness of parasite species to two or more related, although geographically well separated, host species, is illustrated. All through the order from Marsupials to Quadrumana this condition is again and again exemplified. I am then, naturally, made more certain of the essential truth of the thesis, and can the more strongly recommend the attention of systematic zoologists to that practical application of it, which I have stated in the form of a corollary.

REGENERATION, VARIATION AND CORRELATION IN THYONE

PROFESSOR JOHN W. SCOTT

UNIVERSITY OF WYOMING

IT is well known that many Echinoderms possess a remarkable power of regeneration, and the results given here show some interesting phases of this process in *Thyone briareus* (Leseur). The problem was suggested a few years ago in connection with class work in the Marine Biological Laboratory at Woods Hole, Massachusetts. There it is a common practise for students who are taking the invertebrate course to keep aquaria in which are placed specimens brought in from various collecting trips in the vicinity. Students are encouraged to study the behavior of these animals, but their enthusiasm for collecting frequently causes them to overcrowd their aquaria, with disastrous results. After collecting Thyone, especially if they are kept in stagnant water, the student is frequently amazed to find one or more of his specimens that have undergone evisceration. In this process the animal not only loses the principal feeding organs, the tentacles, and the entire digestive system, consisting of the esophagus, stomach and intestine; but it also throws out a whole series of organs surrounding the esophagus including the circlet of calcareous plates, the nerve ring forming the central nervous system, the portion of the water-vascular system known as the ring canal with its attached stone canal and Polian vesicles, and the muscles which serve as retractors for the set of organs surrounding and attached to the esophagus. We shall refer to these muscles as retractors of the esophagus.

The remainder of the animal after evisceration consists, principally, of the dermo-muscular integument, the

cloaca with its attached respiratory trees, the single gonad, the radial canals of the water-vascular system and the major portion of the dorsal mesentery by which the intestine was suspended. Since this part of the animal continues to give reactions, the student invariably raises the question, "Can Thyone regenerate the lost parts?" This question was the starting point of the following investigation. The work had not proceeded far when it was discovered that important individual differences occurred, and the question became, "To what extent, or how completely, may these individual variations be reproduced in the process of regeneration?" Curiously enough, the most important differences between individual Thyone involve structures which help to form the radial symmetry of the animal. Consequently the problem has a bearing on the phylogeny as well as the ontogeny of Thyone.

In general, the results show that regeneration of all lost organs may occur and that there is a decided tendency to even reproduce individual variations. It was found that the Polian vesicles varied greatly in number, size and location. The retractor muscles in a single radius were single or multiple, and for each individual this variation was closely correlated with a corresponding variation in the number of Polian vesicles. Whether one or more Polian vesicles are present, there is a strong tendency for these to occur on the left side of the animal, a fact which undoubtedly has a phylogenetic significance. A more complete statement and a discussion of these results will be given in the following pages.

General Structure of Thyone

Thyone is functionally a bilateral animal. It has anterior and posterior ends, dorsal and ventral surfaces, and consequently right and left sides. The external opening of the genital duct is located near the anterior end in the mid-dorsal region. The structure and arrangement of the tentacles is alike on both sides of the animal. Even

the feeding reactions, as Pearse has pointed out, indicate a bilateral type. The single genital gland is median in position; the genital duct and the stone canal are in the median dorsal mesentery; a part of the intestine and the stomach are supported by the same structure. The respiratory apparatus is also a bilateral structure, one branch arising from each side of the cloaca.

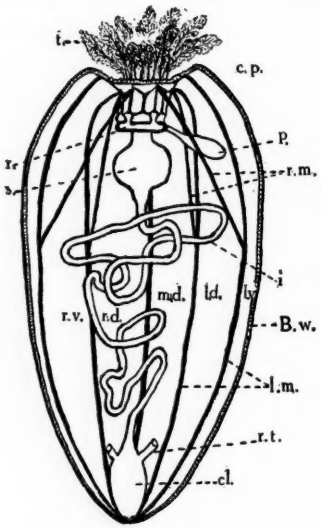

FIG. 1.

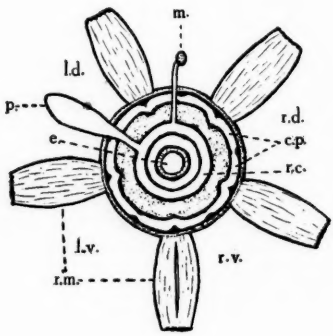

FIG. 2.

FIG. 1. A DIAGRAMMATIC DRAWING FROM A DISSECTION MADE BY TAKING A LONGITUDINAL CUT IN THE BODY WALL A LITTLE TO THE LEFT OF THE MID-VENTRAL LINE. Shows the arrangement of the chief organs concerned in evisceration and subsequent regeneration. *B, w.*, body wall; *cl.*, cloaca; *c. p.*, calcareous plates; *i.*, intestine; *l.* m., longitudinal muscles; *p.*, Polian vesicles; *r.*, ring canal; *r. m.*, retractor muscles; *r. t.*, base of respiratory tree; *s.*, stomach; *t.*, tentacles; *m. d.*, mid-dorsal; *l. d.*, left dorsal; *l. v.*, left ventral; *r. d.*, right dorsal, and *r. v.*, right ventral, interradial spaces.

FIG. 2. A DIAGRAM TO SHOW THE RELATION OF RADIAL TO BILATERAL SYMMETRY. The esophagus (*e*) is shown in cross-section, cut just anterior to the stomach, and the view looks toward the anterior end. *M.*, madreporite; *r. c.*, ring canal. Other letters as in Fig. 1.

Notwithstanding this general tendency toward bilateral symmetry, the most conspicuous differences between individuals involve structures of the radial type. Fig. 1 is a diagrammatic drawing of a dissection to show the general

arrangement of some of the more important structures studied in this experiment. The dissection was made by making a longitudinal cut in the body wall a little to the left of the mid-ventral line, and then pulling the flaps apart and pinning the animal down on its dorsal surface. The Polian vesicle is shown attached to the ring canal in the position where it is usually found when only one is present, that is in the left dorsal interradial space. It will be noticed that the retractor muscles are simply branches of the longitudinal muscles, and hence are radial in position. At the time of evisceration the body wall breaks a short distance posterior to the tentacles, the retractor muscles separate at the point where they join the longitudinal muscles and the intestine breaks off just in front of the cloaca.

A better understanding of the radial type of structure will be gained by a reference to Fig. 2. This figure is a diagram to show the relation of the radial to the bilateral symmetry. The dorsal side of the animal is represented toward the top of the page, the esophagus appears in cross-section, cut just anterior to the stomach, and therefore one is looking forward to the other organs shown. The retractor muscles, showing the position of the radii, are much contracted and thickened, a condition in which they are usually found after evisceration. The stone canal ending in the small madreporite is located in the mid-dorsal interradial space. Passing around in a clockwise direction, the other interradial spaces are designated as right dorsal, right ventral, left ventral and left dorsal. Polian vesicles may be found in any of the interradii except the mid-dorsal space which always bears the stone canal. Although only one Polian vesicle is represented in this figure, the mid-ventral retractor muscle is shown double, a split condition which is characteristic when two or more Polian vesicles are present. This description will be sufficient to show the general relation between the radial and the bilateral symmetry.

EVISCERATION

Only one method of producing evisceration was used. By placing a number of Thyone in a small aquarium of stagnant sea water, the supply of oxygen is soon exhausted. The animals become greatly distended, they crawl up on the sides of the aquarium when possible, and extend the siphon toward and frequently above the surface of the water. All of their behavior, including the pumping of the siphon, indicates that respiration is inadequate. In the course of a day or two the water becomes very foul; soon some of the Thyone will eviscerate, and a considerable percentage will do so as conditions grow more unfavorable. Many, however, resist the unfavorable surroundings and will not eviscerate though kept for several days in foul water. But if the aquarium is now placed where it will have a continuous stream of water and air bubbles passing through it, the behavior of the animals is somewhat different. They then tend to contract to a minimal size, and sometimes assume a volume not more than one fifth to one seventh of their maximum distention. The respiratory movements are practically discontinued; the animal seeks a position as close as possible to the side and bottom of the aquarium. Contraction does not always take place immediately. To my surprise, after several hours I found Thyone which had resisted the previous unfavorable conditions now discharging their viscera. After remaining two or three days in the running water, and the animals had apparently become adjusted to this condition, I again set the aquarium to one side partly filled with water. Then, by repeating the conditions of the first experiment, as the water became foul several more of the holothurians apparently found life too strenuous to further retain their internal organs. When the remainder of this lot of Thyone was returned to running water, and again to stagnant water, a few additional individuals underwent self-mutilation. Out of a total of sixty-one specimens used in this lot forty of them eviscerated. That is, autot-

omy occurred in at least sixty-five per cent. of Thyone, under the conditions described. Probably one reason why this process did not occur in a still larger number is that some animals occupied more favorable positions in the aquarium. A discussion of the cause of evisceration will be given later.

When evisceration occurs it is sometimes hard to see just how the process takes place. Pearse ('09) ascribes the process to a "structural accident"; that is, it is due to a powerful contraction of the circular muscles at a time when the calcareous ring is well forward. "But if the tentacles are extended," he says, "and the calcareous ring is pushed forward a break may occur at *b*" (a point in his Fig. 2 where the body wall joins the calcareous ring) "as a result of the strong contraction of the circular muscles at that point, and the visceral organs are forced out. . . . Whether this autotomy takes place or not depends upon the breaking of the inner branch of the longitudinal muscle bands, whose normal function is to retract the calcareous ring. When the strain brought about by the contraction of the circular muscles becomes too great these inner bands are torn asunder, usually at the point *x*" (inner end of the retractors of the calcareous ring). While it is true that muscular contraction and consequent pressure undoubtedly plays a prominent part in the process, close observation has convinced me that this is not the only factor causing evisceration. Upon several occasions I have watched carefully the breaking of the body wall near its attachment to the calcareous ring, and while there are times when the pressure appears to be strong, especially when the animal is being irritated mechanically, there are other times when the skin appears to "melt away" or separate with very little or no pressure present. Indeed, after the skin once breaks at one side and the viscera escape through the opening, the pressure is relieved. But one may observe that the skin continues to break until the calcareous ring is entirely separated. This, of course, would not happen if the process

depended entirely upon an accidental structural defect. Another thing noticed is of interest in this connection. When splitting open the body wall of an animal that was eviscerating, and thus relieving any internal pressure that might be due to contraction of the circular muscles, some of the retractors were seen still attached to the longitudinal muscles. Under these conditions it would not be possible for the retractors to exert any pull against the pressure produced by the circular muscles, yet the retractors were observed to constrict off or break away from the longitudinal muscles by what appeared to be purely a local disturbance. It is hard to see how this could happen, or how the skin continues to separate around the calcareous ring after the first break is made, if the process of evisceration depends solely upon the breaking of retractors and internal pressure. Indeed, the view that local changes take place in the tissues is supported by other facts. Leptosynapta, if left in stagnant water or under other favorable conditions, undergoes repeated autotomous fission as the result of local constrictions, and Pearse states that autotomy depends upon the presence of the anterior portion of the body, and presumably upon the presence of the circumoral nerve ring. However, he found in Thyone that highly irritating substances like acetic acid and clove oil did not produce ejection of the viscera.

Nor were drugs like codene and atropine, which cause violent peristaltic waves of contraction to pass over the body, any more potent in inducing autotomy. The same may be said of sodium chloride, atropine and clove oil, although the injection of any of these substances was often followed by a waving of the oral tentacles to perform feeding movements, thus bringing about favorable anatomical relations for autotomy.

These results would indicate that the nervous system is not primarily involved. Certainly the ejection of viscera may occur in Thyone without any visible external stimulus.

The parts eviscerated in Thyone have already been

mentioned. However, sometimes evisceration is incomplete, as the following examples will show. On the morning of August 4, a Thyone, which we shall later speak of as individual *H*, was found eviscerating in an overcrowded aquarium jar. While the process usually requires only a few seconds, or at most a few minutes, the intestine in this case was not completely thrown out until two or three hours later. This animal lived until killed at the end of twenty-one days. In the afternoon of the same day on which individual *H* eviscerated, another Thyone was found with the process only partially complete. Five hours later the intestine was still retained, and scissors were used to cut it off at its anterior end near the stomach. Though this Thyone received equally good care it died at the end of two days without further evisceration. A third specimen was found incompletely eviscerated on the above date, but it was allowed to stand until the next morning; at this time the injured end was open, the intestine was still within the body cavity and a part of one of the branchial trees was protruding. The intestine was pulled out and broken off, after which the branchial tree was retracted and the injured end partially closed. This animal also died at the end of two days. A fourth Thyone was seized and by squeezing was forcibly caused to throw off the usual parts except the following: a part of the stomach, most of the intestines, and some of the retractor muscles which had broken off near their esophageal end. The next morning it had expelled the remainder of the stomach and intestine, two complete retractor muscles, and some débris which had escaped from the intestine into the body cavity. The anterior end of the part remaining appeared ragged and imperfectly closed. It died on the third day. It is probable that the two retractor muscles last expelled were broken off at their posterior ends by local constriction, not when the body was under pressure. A fifth animal, which we shall designate as individual *M*, was found partly eviscerated

late on the afternoon of August 6. The next day it still retained the stomach and intestine and at noon the digestive tube was clipped off with scissors in the region of the esophagus. Nothing peculiar was noted in its behavior until four days later, August 11, when it discharged the remainder of the digestive tube. It lived and was killed at the end of eighteen days. These results are typical. The animal dies unless it is itself able to eliminate all organs concerned in the process of evisceration, and therefore regeneration does not occur unless all these organs are eliminated.

The eviscerated animals show comparatively a low degree of mortality. In an attempt to raise twenty-five mutilated Thyone seven died; three of these were unable to complete the process of evisceration as described above, and two more, since they lived for fourteen days, probably owe their death to other causes. The sixth specimen to die lived three days and had been slow in eviscerating. The seventh did not receive the best of care and died after three days. So considering the amount of injury the mortality is extremely small where proper care is taken and evisceration is complete.

It will not be inopportune to describe the subsequent behavior of the different parts after evisceration. The parts expelled lie on the bottom in a more or less inactive condition until they die, which happens usually in the course of a few hours. At first the tentacles frequently expand and contract. They are highly sensitive, as one would expect, and if touched withdraw quickly into the esophagus and at the same time the retractor muscles will undergo strong contraction. By supporting these parts near the surface of the water, so as to insure plenty of oxygen, an attempt was made to keep them alive. In some cases the parts remained alive for two or three days, so this experiment appeared to be partially successful. Death is probably due to the direct exposure of tissues to the sea water and to the attacks of minute organisms. The dermo-muscular portion of Thyone is

much less sensitive than the expelled portion, just after evisceration. This is due to lack of a central nervous system.

Behavior During Regeneration

After evisceration each specimen was placed in a separate jar of fresh sea water. The injured end of the body turns in and closes up tightly, and the entire body is somewhat smaller than before evisceration. Respiration is slower and not so vigorous. If the water is stagnant, within a few hours the animal usually climbs up on the side of the aquarium by means of its tube feet. This part of the animal therefore is capable of responding to a lack of oxygen, and the reaction is independent of the central nervous system.

The observations upon the following individual, referred to in my notes as Thyone *A*, will serve to illustrate the general behavior during regeneration:

July 14, A.M.—Animal eviscerated itself in the usual way. In the afternoon it climbed up on the side of the jar and clung there evidently for the purpose of respiration.

July 15–16.—Acts as on the afternoon of the fourteenth. Keeps closed and well contracted at the injured end. Entire body somewhat smaller than before evisceration, due in part to organs lost. Respiration slower and not so vigorous as normal.

July 17.—In the afternoon, after water was changed, Thyone took up position on the sand against the side of the jar farthest away from the source of light.

July 18.—The next morning it was half buried in the sand in same position, with a few pieces of débris pulled over it. Remained so all day.

July 23.—For some two days it has been slowly burrowing down until only the two protruding ends of the body can be seen. When a piece of débris that was being held over a part of the anterior end was touched, this end retracted below the surface and the posterior end withdrew until it could scarcely be seen. Later the posterior end retracted when the shadow of my hand passed over it, the hand being held about one foot away. The uninjured animal is even more sensitive to shadow. The respiratory movements are growing stronger.

July 28.—For the past two or three days the Thyone has been slowly moving through the sand in a posterior direction without uncovering itself.

August 2.—It is now oriented with respect to the direction of the light and has reached probably the darkest portion of the jar.

August 7.—Has advanced still farther. Came about half way out of the sand to do this.

August 8.—Reacts quickly to shadows by withdrawing, and to jarring the table. Evidently is recovering its normal behavior.

August 10.—Has again come up about half way out of the sand. Reacts quickly to shadows as before.

August 11.—Came entirely out of the sand. Spent the day on the sand or on the side of the jar. Appeared restless.

August 12, 4 P.M.—Has been clinging to the side of the jar and moving about more or less all day. Respiratory movements are strong and apparently normal. Has just now expanded the anterior end sufficiently for me to see the new growth of tissue formed around a pentagonal opening. Fifteen minutes later it was observed to extend a set of minute tentacles and go through feeding movements. The tentacles appeared to be slightly more than three eighths of an inch in length. Its behavior continued apparently normal until it was killed twelve days later.

The actions of other Thyone were studied under the same conditions, and we shall now give a general summary of their behavior during regeneration. The earliest reactions after evisceration take the form of contractions resulting in the closure of the wound, and movements in response to lack of oxygen. If the oxygen supply is sufficient Thyone will draw itself closely into the angle between the side and bottom of the aquarium, or if the supply is deficient, it clings close to the side of the jar near the surface. In from three to seven days an instinct to burrow usually asserts itself. There is a tendency for the body to contract very noticeably at this time, and the whole organism becomes rather inactive. This condition is probably necessary for the formation of new tissue. Pearse makes the statement that in burrowing the normal Thyone will cover itself in from two to four hours. My observations on the mutilated animals indicate that they require from twelve to twenty-four hours, in one case forty-eight hours, to complete the reaction. The process frequently stops for some hours and occasionally is never completed. In the Thyone de-

scribed above the animal did not begin to orient itself with respect to the source of light until about the twelfth day, but in another case the response took place on the second day, which shows that this reaction does not depend upon the central nervous system. It should be stated that normal Thyone similarly placed were used as controls. Thyone *A* was quite sensitive to shadows and to touch on the ninth day, but it reacted more quickly on the twenty-fourth day both to shadows and to mechanical disturbances. Whether this was due to the regeneration of a new central nervous system, or to a more highly developed specialization of function in the old tissue, I am unable to say. It is quite possible that both factors were involved. Respiration is undoubtedly correlated with the activity of the animal, and feeding movements do not occur until the regeneration of all organs is well established, at about twenty-seven or twenty-eight days.

The internal changes that take place during regeneration were studied in animals that were killed at different stages in the process. Thyone *N* was killed nine days after self mutilation. At the injured end there was a very small plug of tissue representing the newly formed esophagus; a thread-like continuation of this tissue, the beginning of a new stomach-intestine, was also seen in the mesentery. The calcareous ring and the ring canal were not clearly defined. Another Thyone was killed at about the same age after evisceration; India ink was injected into the cloaca and into the opening at the anterior end in an attempt to demonstrate a cavity in the newly formed thread-like, stomach-intestine. The results were negative and the esophagus was found to be tightly closed. However, the interesting observation was made that the anterior end of *each of the longitudinal muscles had split off a very slender branch to form a new retractor muscle* (see Fig. 3). These newly formed retractor muscles were not more than one fourth inch in length; their anterior ends were attached in a normal position around the esophagus, but their posterior ends

were attached only a short way back, much in front of the position of attachment of the full-sized retractors. In another animal killed when a day or so older, the same conditions held with reference to esophagus, stomach and intestine. At least three of the radial canals belonging to the water vascular system had branched and connected at their anterior ends in such a manner as to form a part of a new ring canal (cf. Fig. 4). I was unable to find the rest of the ring-canal and perhaps it was not yet complete.

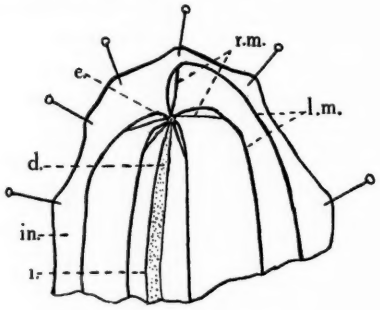

FIG. 3.

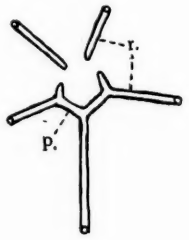

FIG. 4.

FIG. 3. DIAGRAMMATIC DRAWING TO SHOW THAT IN REGENERATION THE RETRACTOR MUSCLES (*r. m.*) ARISE BY SPLITTING OFF FROM THE LONGITUDINAL MUSCLES (*l. m.*). Dissected a little to the right of the mid-ventral line; *d.*, dorsal mesentery suspending the intestine (*i.*); *in.*, integument; *e.*, region of esophagus.

FIG. 4. TO SHOW THE DEVELOPMENT OF THE PENTAGONAL CANAL IN A THYONE ABOUT NINE OR TEN DAYS AFTER EVISCERATION. *r.*, radial canal; *p.*, pentagonal canal. The anterior ends of the radial canals fork dichotomously, and these branches anastomose to form the canal which later assumes a circular shape around the esophagus.

Thyone *F*, which was killed twelve days after evisceration, showed minute calcareous plates which formed a very small esophageal ring not more than one millimeter in diameter. The esophagus continued posteriorly in the form of a small tube, the stomach-intestine, which was suspended in the dorsal mesentery. This new digestive tube was about 0.5 millimeter in diameter and contained small, colored, movable particles that could be seen with the unaided eye. The ring canal was completely formed.

Another specimen, Thyone *O*, died at the end of four-

teen days and was in bad condition when examined. The stomach had begun to expand and retractor muscles were present. Probably owing to the condition of the specimen, no calcareous ring, ring canal, or Polian vesicle could be found. Another individual killed at about fifteen days showed the stomach slightly enlarged, and the intestine, retractor muscles, calcareous ring, tentacular canals, and ring canal well formed. Two small Polian vescicles each about one millimeter in length were present. The position of the new intestine was described in my notes as follows:

> From the stomach the intestine follows the ventral edge of the dorsal mesentery, lying ventral to the gonaduct. At the gonad it turned ventrally with the mesentery and then forward for about one half inch to the left interradial space; here it turns rather abruptly backward, continuing in the mesentery below the left branchial tree to the anterior ventral part of the cloaca.

At a little later stage in another specimen the intestine passed from the left ventral interradial to the right ventral interradial space; then posteriorly and again to the left, following the ventral radial mesentery to the anterior ventral side of the cloaca.

We see from the preceding description that all important organs have been reproduced in form though not in size, before the end of the fifteenth day. The first madreporite with its tiny stone canal was found some eighteen days after mutilation. Twenty-one days after evisceration in one specimen the calcareous ring was about three millimeters in diameter and the ampullæ at the bases of the tentacles were well developed. Within a week after this time the regenerating animal begins active feeding. Thyone *A*, killed at 41 days, was practically a normal animal both in behavior and appearance, except for the fact that the regenerated organs had not yet reached full size. The stomach was about one third normal size, but the Polian vescicles were better developed. The intestine contained a small amount of food material and was nine or ten inches in length; most of this growth had

taken place posterior to the gonad. It was held in position as previously described and had several additional coils.

INDIVIDUAL VARIATIONS

To all outward appearances any two Thyone are as much alike as two peas. It was not until the internal organs were studied that important differences were ob-

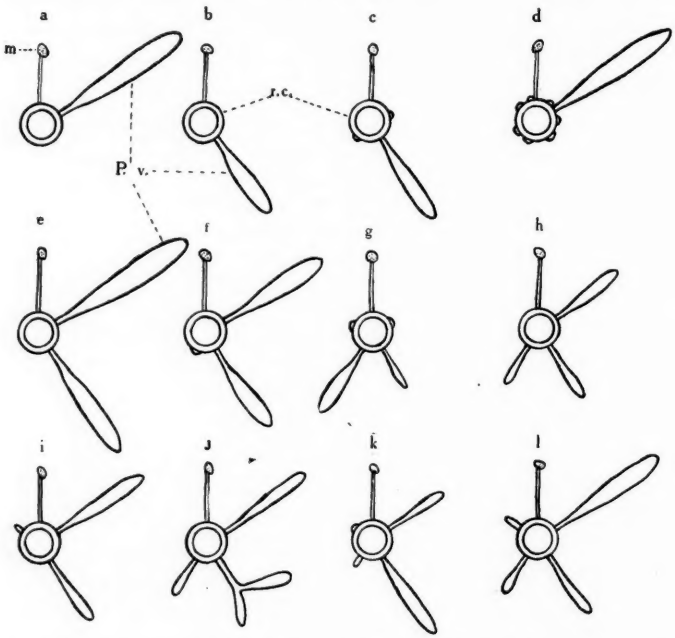

FIG. 5. DIAGRAMS TO SHOW VARIATION IN POSITION AND SIZE OF THE POLIAN VESICLES. *P. v.*, Polian vesicles; *m.*, madreporite; *r. c.*, ring canal; *a-d*, with one Polian vesicle, *e-g*, with two; *h-k*, with three, *l.*, with four; *c., d., f., g., k.*, with additional rudiments of these vesicles; *j.*, with a branched vesicle.

served. While there are numerous minor differences, the most conspicuous variations are found in the number, size and location of the Polian vesicles (cf. Fig. 5), and in the number and arrangement of the retractor muscles. On account of the radial structure of Thyone not more than four Polian vesicles are present, since

a homologous structure, the madreporite and its stone canal, occupies the dorsal interradial space. The number of vesicles varies in fact from one to four. By a reference to Table I, it will be seen that out of 77 individually examined, 41 had one, 20 had two, 14 had three,

TABLE I

TO SHOW THE NUMBER OF POLIAN VESICLES PRESENT IN A GIVEN NUMBER OF THYONE. ALSO TO SHOW THEIR LOCATION IN THE INTERRADIAL SPACES, WITH REFERENCE TO THE BILATERAL SYMMETRY OF THE ANIMAL

Number of Polian Vesicles	Number of Individuals Examined	Left Dorsal	Left Ventral	Right Ventral	Right Dorsal
1	41	38	3	0	0
2	20	17	19	3	1
3	14	14	15	12	1
4	2	2	2	2	2
Totals.....	77	71	39	17	4

and 2 had four Polian bodies. If one is to test the matter of regeneration, of course it is important to know whether the variations or individual peculiarities will be accurately reproduced. Another striking characteristic comes out when we note in the same table the location of these organs. Of the forty-one individuals which had a *single Polian vesicle, all were on the left side of the animal,* and 38 were in the left dorsal interradial space. In twenty specimens with two Polian bodies each, 36 were on the left side and only four on the right side of the body. A similar asymmetrical distribution of these parts was found when three Polian bodies were present. In one specimen, however, two vescicles were found in one space, the left ventral interradius, the only instance of this kind observed; on account of this doubling, the right side lacked one of the number to which it was entitled in the table. Where four Polian bodies are present the arrangement is, of course, symmetrical on both sides. Still another interesting fact comes out when we examine the totals in the last line. Out of the 77 individuals, 71 had a Polian vesicle in the left dorsal interradial space, 39 vesicles were found in the left ventral,

17 in the right ventral, and only 4 in the right dorsal space. That is, the total number on the left side compared with the total number on the right side bears the ratio of 110 to 21. Not only is there this tendency for the vesicles to be more abundant on the left side of Thyone, but the totals show that *the chances of a given Thyone having a Polian vesicle in any given interradial space decreases in a counter-clockwise direction,* beginning with the left dorsal interradial position. Coinciding with the number of individuals examined, the maximum number of chances is found in the mid-dorsal interradius, where the stone canal is always present. That is, the stone canal with its madreporite is a more fundamental and stable structure than each or all of the vesicles.

The conditions are none the less interesting when we compare the Polian vesicles with reference to size and location, as will be seen from the examination of Table II. The Polian vesicles are here divided arbitrarily into three groups, designated as large, medium and small, and their respective locations are shown. In addi-

TABLE II

TO SHOW THE POLIAN VESICLES WITH REFERENCE TO SIZE AND LOCATION

Size	Left Dorsal	Left Ventral	Right Ventral	Right Dorsal	Total
Large.....	56	17	0	0	73
Medium.....	17	22	5	1	45
Small.....	0	0	10	3	13
Rudiment...	2	1	5	7	15
Total.....	75	40	20	11	146

tion some Thyone had the rudiments of other vescicles, each too small to be considered a distinct pouch. These are designated in the table as a "rudiment." It will be noticed that all of the large, and most of the medium-sized vesicles are on the left side; that all the small ones, and most of the rudimentary ones are on the right side. The table as a whole shows that not only does the number of Polian vesicles diminish in a counter-clockwise

direction, but their size diminishes following the same law. These facts appear significant and without doubt are suggestive of ancestral history.

If it is true that the radial symmetry of Echinoderms is to be ascribed to a fixed stage in their ancestral history, we are led to suppose that the point of attachment was on the right side of an originally bilateral animal. The life history of Pentacrinus, the larval organ of Asteroidea, and a great many anatomical and embryological facts support this view. While it is not within the province of this paper to discuss the relative significance of these matters, the evidence is so overwhelming that the theory is generally accepted. It is also no doubt true that some groups of Echinoderms took to a free-living existence early in their ancestral history, and others remained fixed until comparatively a late period. As proof we may cite the embryological evidence that Holothurians develop without any attached stage whatever. that the Asteroids develop a larval organ and pass through a Sessile stage for a brief period in their development, while the crinoids usually remain permanently fixed throughout life. At least we can best account on this theory for the deep-seated and fundamental radial symmetry of some forms; the longer the attachment the more deep-seated would become the type of radial symmetry. Now if this theory is correct we can use it to explain the conditions described above for Thyone. The ancestors of this form must have broken away from the fixed stage very early, for we find the radial symmetry not well established on the right side of the animal as evidenced by both the position and size of the Polian vesicles. Out of 118 large and medium-sized Polian vesicles, 112 were on the left side, while in a total of 28 small or rudimentary Polian bodies, 25 were found on the right side. The arrangement of these organs in Thyone adds one more bit of evidence to support the following statement of Lankester.

It therefore appears that the Holothurian stock branched off from the Pelmatozoa before complete pentamerous symmetry of the hydrocoele and associated organs had arisen, before any definite calcynal system had developed, while the gonads were still a simple strand opening to the exterior by a single posterior gonopore.

The muscles used as retractors of the œsophagus were other organs in which there was considerable individual variation. As a general rule each of the five retractor muscles consists of a single band that takes its origin from the longitudinal radial muscle about one third the way back from the anterior end of the body and is inserted in front into the wall of the esophageal ring. Such a retractor, however, is frequently split up into several strands varying from two to five in number. A reference to Table III

TABLE III

TO SHOW THE CORRELATION BETWEEN THE NUMBER OF POLIAN VESICLES AND THE TENDENCY FOR THE RETRACTOR MUSCLES TO DIVIDE

Number of Polian Vesicles	1	2	3	4
Retractor muscles, single	39	2	0	0
Retractor muscles, multiple	1	17	15	2
Average number retractor muscles, per individual	5.153	10.263	12.400	10.000
Average number retractor muscles, per radius	1.030	2.052	2.480	2.000

shows that in 76 individuals examined, 41 had retractor muscles all in single bands, while 35 specimens had these muscles subdivided or multiple in character. This variation is especially interesting when considered with reference to the number of Polian vesicles. For in forty cases where one Polian body was present thirty-nine bore the unsplit or single retractor and there was only one specimen with these muscles showing a multiple number. In thirty-six cases where two or more Polian vesicles were present, all but two had the retractor muscles in a split or divided condition. If we consider each strand as a separate retractor muscle, we may then obtain the average number of retractors per individual for any definite number of Polian vesicles. By a reference to the fourth horizontal line of Table III, one finds that the average number in individuals with one Polian vesicle is

just slightly in excess of five, the pentameric number, and the average number when two Polian vesicles are present is 10.263. This ratio is only partly maintained when three vesicles are present, for the average number is then 12.400, and in the two cases with four vesicles the average was just twice the pentameric number. It is therefore evident from the facts shown in this table that with an increase in the number of Polian vesicles there is associated a strong tendency for the retractor muscles to take on a split character. If it were not for the fact that the split character shows considerable variation in the same individual one might suggest that the tendency to divide is correlated with the greater functional activity of the water vascular system as evidenced by the increased number of Polian vesicles and the location of the longitudinal muscles that lie along and just internal to the radial canals. About all one can say is that correlated with a more complete radial symmetry with respect to the Polian vesicles, there is a greater plasticity in the retractor muscles, causing them to divide longitudinally into separate muscle bands.

To what extent, or how completely, may these individual variations be reproduced in the process of regeneration? An answer was obtained in the following way. First a close examination was made of all parts eviscerated and a record was kept of all organs showing variable structures. Special attention was given to Polian vesicles and to retracter muscles. The mutilated specimens were then placed in separate aquaria in which the water was changed frequently to prevent it from becoming stale. After a considerable interval these animals were killed and the regenerated organs were compared with the lost parts. Table IV shows several individuals compared in this way. The number of retractor muscles found in each radius is given in the order of the radii taken in a clockwise direction. A study of the table indicates that there is a strong tetndency to reproduce individual peculiarities, as shown by individuals *B, E, G, H, M* and *O*. This does

not always hold true, for individual *L* reverted toward the more radial type of symmetry. From these few cases it would appear that individual peculiarities tend to predominate over ancestral influences in the process of re-

TABLE IV

TO ILLUSTRATE THE RELATION BETWEEN REGENERATION AND ORIGINAL SYMMETRY IN THYONE

Individual Used	Original Symmetry		Regenerated Symmetry	
	Polian Vesicles	Retractor Muscles	Polian Vesicles	Retractor Muscles
B	2	2–2–2–2–2	2	3–3–2–3–3
E	2+	3–3–2–2–2	2	2–3–2–2–2
G	2	1–1–1–1–1	2	2–1–1–1–1
H	2	1–2–2–2–1	2+	2–2–2–2–2
L	1	1–1–1–1–1	2	2–3–2–2–2
M	1	1–1–1–1–1	?	1–2–1–1–2
O	3+	2–2–2–2–2	?	2–2–1–2–2
W	..	.....	2	2–2–2–3–4
X	..	.....	2	2–2–2–2–2
Y	..	.....	2	2–2–1–2–2

generation. Specimens *W*, *X*, *Y*, are included in this table to show further the correlation between Polian vesicles and retractor muscles.

DISCUSSION AND SUMMARY

There remains to be discussed the general bearing of the foregoing experiments. First, the difference in the number of Polian vesicles in different Thyone is partly compensated by a variation in size, the fewer the number the larger their size, though this ratio would not be an exact one. In other words the total volume of the Polian vesicles in any given specimen bears a general relation to the size and functional activity of the animal. Notwithstanding this functional relationship since the actual number varies so widely it would be interesting to compare the number found in other species of holothuria with the conditions in Thyone. The data secured on this question were meager and not very definite. For example, Packard in one of the older text-books says in speaking of Thyone,

There are three Polian vesicles, one fusiform and an inch in length, the two others slenderer.

Clark ('02) gives the number for *Thyone briareus* (Leseur) as usually one or two; for *T. scabra* (Verrill) as usually single, and for *T. unisemita* (Stimpson) as one. He also mentions six other holothurians found in the Woods Hole region and all have a single Polian vesicle except *Cucumaria frondosa* (Gunnerus), which usually has one. He says nothing of the position in which these vesicles are found. In another paper ('01) Clark mentions a large holothurian about 40–45 centimeters in length (*Holothuria mexicana* Ludwig) in which there is a great diversity in the number of tentacles and Polian vesicles. The tentacles vary from 18 to 21, while the Polian vesicles vary from 1 to 9. The number of specimens examined, sixteen, was hardly sufficient to obtain an adequate comparison; two had 1 vesicle each, two had 2, five had 3, three had 7, one had 8, and one had 9. It is probable that if one were to examine a large number of individuals of each species, with reference to the number and location of the vesicles, he would obtain further interesting results. Lang ('96) cites a number of groups of holothurians in which only one vesicle has been observed; but states that there are a number of species in other groups that have occasionally or usually more than one.

Where accessory vesicles occur they vary greatly in number, and appear to have very slight, if any, systematic significance. Where only one Polian vesicle occurs it lies in the left ventral interradius, very seldom in the left dorsal interradius. Where two or more vesicles occur, they are also mostly formed in the ventral region of the circular canal.

Since Lang describes Cucumaria as the type specimen, in which the Polian vesicle is said to be in the left ventral region, it is possible that his generalizations were based principally on this form. At any rate, the conditions in Thyone seem to give a more definite significance to the number and location of the Polian vesicles.

Various explanations of autotomy and evisceration have been suggested, many of them having a teleological character. The view that the holothurian offers up the better

part of itself to appease the hunger of its enemy lacks confirmation, since the viscera are distasteful to fishes and to some other animals. It may be that the autotomous elimination of the Cuvierian organs serves a defensive purpose, as pointed out by Ludwig and Minchin, and Minchin suggests that the viscera may also be lost in this process and thus incidentally be associated with a protective response. In the case of Thyone, however, evisceration can hardly be considered defensive, and certainly it is not a process of self-division for only one part produces a new individual. Clark ('99) in discussing self-mutilation in the synaptas states the matter clearly in the following terms:

> I agree entirely with Cuenot ('91) in believing that autotomy is not normal or defensive but is due entirely to pathological conditions. I never saw a case of it in synaptas supplied with plenty of sand and an abundance of sea water.

Lang ('96) points out one of these pathological conditions, and recounts the fact that

> A Stichopus was observed to come entirely out of its skin, *i. e.*, the whole integument dissolved into slime, so that only the dermo-muscular tube enclosing the viscera remained.

In the present paper I have mentioned that Thyone at times appears to undergo a similar softening of the tissues in the region where the break occurs, and Pearse ('09) showed that autotomy is due, at least in part, to a structural arrangement which he considers is accidental in character. My observations further show that local constrictions undoubtedly have an important part in separating the retractors from the radial longitudinal muscles. All of these factors are pathological and are due to external or internal stimuli. The external (extra-cellular) stimuli, mechanical and chemical, as tried by Pearse ('08), appear to be less effective in producing autotomy than the purely internal (intracellular) stimuli such as lack of oxygen and its associated phenomena. The chemical (strychnine) that produced the largest percentage of evisceration in Pearse's experiments, probably affected respiration, since it greatly increased the activity of the

animal; therefore the need of oxygen would be proportionately greater than the supply, and the Thyone rendered more susceptible to evisceration. Now while autotomy undoubtedly enables the animal to maintain its existence for a considerable period on a smaller supply of oxygen, the times when this would become necessary in nature are probably rare, and it would be futile to speculate upon what evolution yet has in store for the process.

According to Lang, the retractor muscles of the oral region have been derived by the splitting up of the originally simple longitudinal muscles, and this specialization became more marked as the oral tentacles became more highly developed and required increasing protection. Species are to be found in the Dendrochirotæ in which the separation and branching off of retractors from the longitudinal muscles has not yet been perfected. In regeneration the retractor muscles of Thyone are derived in the same way, *i. e.*, by splitting off from the longitudinal muscles, and such progress is made that they are fairly well developed by the time the tentacles take up the function of feeding. The increasing sensitiveness and the later activity of the regenerating animal are presumably associated with the development of a new nervous system.

If we may regard the bilateral echinoderm larva as representing an early phylogenetic stage rather than a larval adaptation to a free-swimming existence, we will now discuss the symmetry of Thyone. As stated above, it is generally agreed that the radial arrangement of parts of the echinoderm body is due to a fixed stage in its ancestral history. Some holothurians and spantangoids, show in their ontogeny first a free stage, second a radial stage, and finally a bilateral adult. During the development of asteroids that have a fixed embryonic stage, the early bilateral symmetry is soon disarranged by the development of organs on the left side of the animal. For example, the left hydrocœle takes the form of an unclosed water-vascular rosette which grows around the esophagus to form the ring canal and its appendages, and its connection with the dorsal pore gives rise to the stone

canal. Excepting the echinoids and crinoids in which there is either no distinct Polian vesicle or else a simple glandular structure, those echinoderms that have retained the most distinctive type of radial structures have also as a rule, retained the most symmetrical arrangement of the Polian vesicles. Presumably these forms, the asteroids and ophiuroids, have quite recently abandoned the fixed stage, and each individual usually has four Polian vesicles and a stone canal, one in each interradius. Among most of the holothurians a secondary bilateral symmetry has become superimposed over the radial type, and it is reasonable to suppose that there was a time in the ancestral history of Thyone when the Polian vesicles were symmetrically and radially disposed, or else the animal quit its fixed habits before the radial symmetry of the vesicles was thoroughly established. In the one case we would have a regression, a sort of backward retracing of the steps of evolution, or, which seems more probable, the ancestors of Thyone began a free-living existence before the radial arrangement of the Polian vesicles had become complete. Also the fact that the embryology of the holothurian egg is probably much compressed and shows no trace of a fixed stage indicates that the corresponding ancestral stage was comparatively short, or, very remote. Since the modern habits of Thyone are bilateral, and since it is altogether improbable that such habits would produce the present arrangement of Polian vesicles, the position of these organs must be due to ancestral influence.

Now the Polian vesicles are capable of contracting and expanding and their function when they are well developed is to act as accessory reservoirs of the water-vascular fluid. Muscle and connective tissue in the wall of the vesicle furnish the means to do this work. Of course, if the ampullæ are well developed there is little or no need of Polian vesicles, as is the case in Asterias. But, though the size and number of these vesicles is functionally correlated with the general development of the water-vascular system, especially of the oral tentacles,

and hence shows great variability in the different species of holothurians, this does not in any way explain the great excess of these vesicles on the left side of *Thyone briareus*. In regeneration, probably through the influence of functional correlation, there is a tendency for the old tissue to reproduce the exact number and arrangement of the lost vesicles, but it may reproduce a somewhat more radial (ancestral) arrangement.

Enough has been given in this paper to show the need of a more extensive and intensive reexamination of the Polian vesicles. This would give a better idea of their morphological and functional significance. The following summary and conclusions are based on the work described:

1. Evisceration in Thyone includes the following organs: Esophagus, stomach, intestine, calcareous ring, nerve ring, tentacles, ring canal, Polian vesicles, stone canal with madreporite, and the retractor muscles of the esophagus.

2. The method used to produce evisceration was to allow Thyone to stand in stagnant water until it became foul. This was followed by treatment with running water containing much oxygen. Alternating these processes produced as high as 65 per cent. of self-mutilated individuals.

3. The structural accident theory of Pearse is inadequate to explain all of the conditions arising in the process of autotomy. At times the skin appears to dissolve away with little or no pressure present, and retractors frequently break off by local constrictions instead of by longitudinal pull.

4. The parts eviscerated are at first highly irritable, and may be kept alive for some time. The part remaining is less responsive, but reacts to touch, to lack of oxygen, and probably to other stimuli.

5. Regeneration of all lost organs may occur, but it takes place only when all parts concerned in evisceration are completely expelled. Otherwise the animal dies.

6. During the process of regeneration the behavior gradually becomes more responsive and finally is like the normal individual. This appears to be correlated with the growth of a new nervous system.

7. Thyone is functionally a bilateral animal, but the most conspicuous individual differences involve structures that have a radial arrangement.

8. The Polian vesicles vary greatly in number, size and location. There is a strong tendency for these to occur on the left side, and this arrangement is undoubtedly due to ancestral conditions, for the present bilateral habits of Thyone could probably have no influence in producing this asymmetry.

9. The retractor muscles in a single radius consist of single or multiple strands, and this variation is closely correlated with a similar variation in the number of Polian vesicles. No explanation is forthcoming for this peculiar plasticity of the retractor muscles, but the suggestion is made that it may be functionally correlated with the development of the water-vascular system.

10. It was found from the study of a number of specimens that individual peculiarities of structure tend to be reproduced in the process of regeneration. In this process it would appear that individual variations tend to predominate over generalized ancestral influence.

11. Autotomy enables Thyone to survive for a considerable period on a smaller than normal supply of oxygen. Nevertheless, the conditions which give rise to self-mutilation are seemingly in all cases pathological.

12. The conditions in Thyone afford some evidence for believing that when this animal abandoned the fixed stage the Polian vesicles conformed more or less to the radial type. This is opposed to the statement of Lang that in all cases where a multiple number is now present "there was originally only one vesicle." It is believed that the present arrangement of Polian vesicles in Thyone can be best accounted for on the theory of phylogenetic influence. That, in general, those vesicles have retained their most complete radial arrangement in those species of

echinoderms which have maintained to a high degree the functional activity of the water-vascular system.

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SHORTER ARTICLES AND DISCUSSION

TERMS RELATING TO GENERIC TYPES

In the field of biological taxonomy an important reform is in progress. The change is from the method of concepts to the method of types, in order that names may be applied with greater precision and permanence. Under the method of types we no longer think of the technical name of a plant or an animal as attaching primarily to a concept embodied in a description or definition, but as relating to the first representative of the group that became known to science. In determining the application of a specific name we go back to the original specimen or type on which the description was based. The original description has become secondary to the original specimen. In like manner generic names are treated as relating primarily to groups of species, with the original species as the generic type.[1]

Without waiting to appreciate the fundamental nature of the change from concepts to types, many systematic workers took it for granted that generic types were to be determined by elimination, in much the same way that generic concepts had been treated, by gradual subdivision, restriction and removal of component groups. The general results of elimination were the same as under the method of concepts. The applications of many of the older generic names did not become definitely fixed, but remained dependent upon varying individual opinions of the validity of the work of later authors. It often happened that after elimination was accomplished only the doubtful or unidentifiable species remained to serve as generic types. Gradually it became apparent that the practise of elimination was inconsistent with the method of types, and could not insure stability in the application of names. Recourse was then had, especially by zoologists, to the arbitrary designation of generic

[1] Cook, O. F., 1898, "The Method of Types," *Science*, N. S., 8: 513; also 1900, "The Method of Types in Botanical Nomenclature," *Science*, N. S., 12: 475, and 1902, "Types and Synonyms," *Science*, N. S., 15: 646. Swingle, Walter T., 1913, "Types of Species in Botanical Taxonomy," *Science*, N. S., 37: 864.

types, the apparent object being to preserve the results of elimination, even though the theory had to be abandoned. Probably it is only a question of time until the results of elimination will be discarded, as well as the theory, and replaced by the actual, historical types.

A plan for determining the historical types of genera was adopted in 1907 in the American Code of Botanical Nomenclature, and other applications of the method of types are being recognized by zoologists. Specialists in many groups are engaged in the study of generic types, and the need of a special terminology to facilitate work of this kind is becoming apparent. Thus in Bulletin 83 of the U. S. National Museum, "Type Species of the Genera of Ichneumon Flies," by Henry L. Viereck, two new terms, "isogenotypic" and "monobasic," are employed in treating of the application of generic names to type species. The paper is of interest, not only to students of this group of insects, but also as an example of the tasks that confront all taxonomists who appreciate the need of basing their work upon types. The distinctions to which the special terms refer are undoubtedly useful, and the possibilities of expressing them in more convenient form are worthy of consideration.

The word "isogenotypic," is used with reference to cases where two or more generic names have been applied to the same type species.[2] For this purpose a new term is not needed unless zoologists are unwilling to borrow from botanical nomenclature a more convenient method of treating the same class of cases. The botanical code provides a classification of synonyms, and applies the word "typonym" to a name that has to be rejected because an earlier valid name was proposed for the same type. The formation and use of typonym are in accord with a familiar analogy. As a preoccupied name becomes a homonym, it is easy to remember that the use of a preoccupied type results in a

[2] A different combination might have been expected, such as "autogenotypic" or "deuterogenotypic," since isogenotypic suggests the notion of equally good types or of equal numbers of types, instead of conveying the idea of one and the same type, or of a second use of the same type. Genera have been termed "isotypical" when they were described from more than one species, but all truly congeneric, on the assumption that such species would have equal standing as types. A still older use of the word "isotype" had reference to equal representation of a genus by similar or corresponding species in different geographical regions or geologic periods. See Schuchert, Charles, 1905, U. S. National Museum Bulletin 53, Pt. 1: 16.

typonym. A name based on a different type species, but congeneric with the type of an older genus, is termed a metonym. A name rejected for lack of an identified type is a hyponym, and one rejected for linguistic reasons, a caconym. All rejected names fall readily into these five classes.

The other new term, "monobasic," is used by Mr. Viereck to indicate genera with only one species at the original place of publication. In botanical literature the word "monotypic" is often employed in this sense, though also applied to genera that consist of only one species. If previous use disqualifies monotypic, the same objection lies against monobasic. In addition to an older chemical meaning, the same word was employed several years ago in a biological sense, to describe a condition of descent in simple lines.[3] Apart from being preoccupied, the word monobasic has a misleading implication, since under the method of types each generic name is referred to a single type species. The idea of a genus being based on many types is discarded with the method of concepts. Appreciation of this incongruity may explain why no such term as "symbasic" or "polybasic" is used in contrast with monobasic, to indicate genera that were first proposed in connection with more than one species.

Evidently there is need of a simple and consistent terminology for indicating relations between generic names and type species. The normal relation under the method of types is the designation of the type species at the original place of publication of the genus. Genera provided with types by original designation may be described as *orthotypic*, or normal-typed. With orthotypic genera there is no occasion to raise the question of how many species were included at the original place of publication.

[3] Cook, O. F., and Swingle, W. T., 1905, "Evolution of Cellular Structures," Bull. 81, Bureau of Plant Industry, U. S. Department of Agriculture, p. 20. Plants or animals with specialized habits of asexual reproduction, such as vegetative propagation, parthenogenesis or self-fertilization, would be described as monobasic. The second edition of the Standard Dictionary defines monobasis as follows: "The derivation of a stock from a single parentage by inbreeding, or by propagation of buds or cuttings; opposed to symbasis." Thus the danger of ambiguity in using monobasis for nomenclatorial purposes is greater than in using monotypic, though it must be admitted that the use of the word monotypic in two senses may sometimes result in confusion. Genera that were monotypic in the strictly nomenclatorial sense of being established in connection with one species may not be monotypic in the more general taxonomic sense of including only one species.

Genera that are not orthotypic fall into the two classes already considered, those with a single species at the original place of publication, and those with two or more species. It is now generally agreed that when only one species was mentioned this should be accepted as the type. Such genera may be called *haplotypic,* or single-typed. When two or more species were included in the original treatment of a genus, and no type was designated, we have the problem of subsequent determination of the type, resulting in what may be termed a *logotypic* genus, that is, a genus with a rationally selected type species. The object of selection is to determine the historical type of the genus. Names must have definite applications, and historical applications of generic names can be made definite by ascertaining the historical types. The recognition of a new generic group is usually based on one leading or dominant species, with the others added as associate members.

In many cases the generic type is intimated by the original author in dividing the genus into subgenera or sections, in illustrating one of the species or citing illustrations published in earlier works, in naming the genus with particular reference to one of the species, in recording economic uses, or in giving geographical or other indications of greater familiarity with one of the species. If the application of these or other historical criteria leaves more than one species eligible for selection, the first of the eligible species should be taken as logotype. In this way it is possible to develop a consistent system of type selection that will commend itself as reasonable and give the same results in the hands of different students.[4]

[4] Simply taking the first species under a generic name as the type would probably establish more of the generic names in their historical places than the method of elimination, which accepts the last of the original species left in the genus as the type. Either of these methods of selecting types would result in many cases of separation of generic names from their historical types, but these undesirable changes in the application of names can be avoided by taking the historical considerations more directly into account, as in the American Code of Botanical Nomenclature. Probably a more satisfactory system for associating generic names with their historical types could be developed by sufficient study of the problem. A policy of refusing to revive generic names that were not directly associated with binomial species to serve as types, would avoid many of the changes threatened by unmitigated priority. In proposing lists of "*nomina utique conservanda*" in advance of any provision for the definite application of names, European botanists have demonstrated one more way to put the cart before the horse.

In addition to the three ways of associating generic names with their type species, there are many cases where generic names have been applied to groups that do not include the type, or any of the original species. Formal assignments of erroneous types also occur when generic names are not traced back to their original places of publication, or when ineligible species are designated as types. In dealing with the synonymy of genera previously treated under names that belong to other groups it will be convenient to have a distinctive term for this class of cases. Such misplaced names, applied to groups that do not contain the true type, may be indicated as *pseudotypic*, or false-typed.[5]

It should be expected that more critical analysis of taxonomic problems would lead to more definite distinctions and more precise terms. The older terminology was developed to facilitate the study of names, whereas it is now apparent that provision must be made for the study of types as another formal branch of biological taxonomy. Nomenclature has a history of three hundred years while systematic typology is only beginning. To gain further insight into these typological problems is obviously more important than to attempt premature applications of partial solutions. It may take fifty or a hundred years to transfer

Failure to regulate the application of names is the fundamental defect of the Paris and Vienna codes, and is hardly to be cured without thorough recasting.

[5] Thus the palm genus *Martinezia*, as treated by Kunth, Martius, and many later writers as relating to *Martinezia caryotæfolia* and its immediate relatives, was pseudotypic, for this species does not appear to be congeneric with any of the five species originally referred to *Martinezia* by Ruiz and Pavon. Hence it has been proposed to replace this pseudotypic use of *Martinezia* by a new generic name, *Tilmia*. (See *Bull. Torrey Bot. Club*, 28: 565.) The five original species of *Martinezia* belong to three natural groups, now recognized as distinct families, the first two species to the Cocaceæ, the third species to the Acristaceæ and the others to the Chamædoreaceæ. The third species, *M. ensiformis*, should be taken as logotype of *Martinezia* because the figures used to illustrate the generic characters evidently represent a member of the family Acristaceæ. Another reason for excluding the cocoid species from consideration as type is that they are mentioned as deviating from the "essential characters of the genus," in connection with the original description. The rule of the Vienna code, to the effect that the name of a subdivided genus should go with the majority of the species, would carry the name *Martinezia* over to the family Chamædoreaceæ. The making of such a rule shows that many European botanists were still working under the method of concepts, and were not accustomed to think of generic names as inseparably connected with type species.

the whole structure of biological taxonomy to the new foundation of types. To suppose that any permanent advantage can be gained by elaborating defective methods under forms of legislative enactments or judicial decisions is to show a limited appreciation of the nature of the subject and of its historical development. As long as legislation and interpretation are based on inadequate study, they can represent, at most, only a temporary consensus of opinion, for it is of the very nature of science to condemn and throw aside any doctrine or method that has proven inadequate or fallacious.

Terms Relating to Synonyms

The following classes of synonyms were recognized in 1907, in the American Code of Botanical Nomenclature:[6]

Homonym.—A name rejected because of an earlier application of the same name to another genus.

Typonym.—A name rejected because an older name was based on the same type.

Metonym.—A name rejected because an older valid name was based on another species of the same genus.

Hyponym.—A name not associated with a type.[7]

[6] *Bulletin of the Torrey Botanical Club*, 34: 167, 1907.

[7] Much confusion would be avoided by a consistent policy of withholding recognition of generic names that have not been associated with type species. Thus the name *Acoeloraphe*, proposed by Wendland in 1879 in an analytical key to genera of fan-palms (*Bot. Zeitung*, 37: 147), was not associated with a type, though evidently relating to a species mentioned in the same paper as "*Brahea serrulata.*" This Florida palm differs from the Mexican type of *Brahea* in the leaf characters assigned to *Acoeloraphe* in the key and in the seed character indicated by the generic name, the albumen being solid instead of having a deep channel along the raphe. But *Acoeloraphe* being left without a type, another name, *Serenoa*, was proposed by Hooker f. in 1883 for "*Sabal serrulata* R. & S." (Genera Plantarum, 3: 926). All subsequent writers have accepted Hooker's name, and *Acoeloraphe* should remain under *Serenoa* as a hyponym. Nothing has tended so strongly to bring the principle of priority into disrepute as the incontinent revival of abortive names, to replace properly established names in current use. No species was referred to *Acoeloraphe* until 1907, when Beccari (Webbia, 2: 107) applied the name *Acoeloraphe wrightii* to a Cuban member of a genus that had been described in 1902 under the name *Paurotis*, a Bahaman species, *Paurotis androsana*, being the type (*Mem. Torrey Bot. Club*, 12: 21). This transfer of the name *Acoeloraphae* to the genus *Paurotis* was followed by Sargent in 1911 (Trees and Shrubs, 2: 117), but Beccari's genus *Acoeloraphe* is a metonym of Paurotis, and is also pseudo-

TERMS RELATING TO TYPE SPECIES

Orthotype.—Type by original designation. A species designated as type in connection with an original publication of a generic name. A genus whose type was formally designated at the original place of publication is orthotypic.

Haplotype.—Type by single reference. A single species referred to a genus at the original place of publication, and on this account accepted as the type. A genus proposed with reference to a single species is haplotypic.

Logotype.—Type by subsequent determination. The historical type of a genus, selected from two or more original species. A genus whose type is selected from two or more original species is logotypic.

Pseudotype.—Erroneous indication of type. A species erroneously indicated as the type of a genus. A genus treated on the basis of an erroneous type, or so as to exclude the true type, is pseudotypic.

O. F. COOK

BUREAU OF PLANT INDUSTRY,
U. S. DEPARTMENT OF AGRICULTURE,
March 13, 1914

typic, because of the original application of the name to *Serenoa.* Two species of *Paurotis* are supposed to exist in Florida, one that is identified with the Cuban *P. wrightii* (Grisebach & Wendland) and a local species, *P. arborescens* (Sargent).

NOTES AND LITERATURE

LINKAGE IN THE SILKWORM MOTH

ONE of the most striking recent developments in the study of genetics is the discovery of linkage in many of those forms which were supposedly thoroughly worked out. The most recent example is a very interesting paper by Y. Tanaka,[1] entitled "Gametic Coupling and Repulsion in Silkworms." The data presented in this paper demonstrate the existence in the silkworm moth of a group of four pairs of linked genes. Following Tanaka's nomenclature we may designate these genes as follows: *N*, which differentiates the larval color pattern known as "normal" from that called "plain"; *S*, occurring in larvæ having the "striped" pattern, and epistatic to *N*; *M*, the differentiator for the "moricaud" larval pattern, also epistatic to *N*; *Y*, the gene which differentiates caterpillars with yellow blood and yellow cocoons from the recessive whites. Of the six possible combinations of these genes, taken two at a time, all but *NM* and *SM* were made, and all showed linkage. F_2 "coupling" tests, *i. e.*, from matings where both dominants entered the cross from the same P_1 individual, were made for *SY* and for *MY*. In each case there occurred cross-overs, or new combinations of the characters, in such proportions as to lead Tanaka to suppose the ratio of parental combinations to cross-overs among the gametes to be about as 7:1. "Repulsion" (where one dominant entered from each P_1 individual) F_2 results were obtained for *NS* and for *NY*. In neither case did any double recessives (cross-overs) appear, though over 3,000 caterpillars were obtained in the case of *NY*, and 224 in the case of *NS*. From these data Tanaka concludes that the repulsion was complete in these two cases. It has, however, been pointed out by Morgan[2] that such results will be obtained if the linkage is complete in one sex only. In *Drosophila* such "repulsion" crosses never produce double recessives in F_2, and it has been shown that this is due to complete linkage in the male, crossing over being frequent in the female between some pairs of genes. In order to test this possibility it is necessary to mate doubly heterozygous individuals to double recessives, when the gametic ratio is obtained directly and without the complications present in most F_2 results. It so happens that Tanaka reports two such crosses, one for each sex, though he does not recognize their im-

[1] *Jour. Coll. Agr.*, Tohoku Imper. Univ., Sapporo, Japan, V, 1913.

[2] *Science*, N. S., XXXVI, 1912.

portance in this connection. When a male heterozygous for *S* and for *Y*, one dominant having been derived from each parent (*SysY*), was mated to a doubly recessive (*sysy*) female, there were produced 63 *Sy* and 65 *sY*—no cross-overs. A female heterozygous also for *S* and for *Y*, but having them "coupled" (*SYsy*), was mated to a male *sysy*, and produced 215 *SY* and 188 *sy*—again no cross-overs. Yet that crossing over may occur between these two pairs of genes is shown by the fact that the "coupling" F_2 results indicated a gametic ratio of about 7 : 1 : 1 : 7. We are, therefore, still left in the dark as to whether crossing over occurs in only one sex, or in both. But it is certain that the strength of linkage in this case is not always the same—a point of great interest and importance. Similar cases have been reported by Baur[3] in *Antirrhinum*, by Punnett[4] in the sweet pea, and by the writer[5] in *Drosophila*.

Tanaka refers to his case as differing from previously reported cases of linkage in animals in that the sex differentiator is not one of the genes involved, and in that the linkage is sometimes only partial. However, he refers several times to a paper by Morgan[6] in which it is clearly shown that three of the sex-linked genes in *Drosophila* also show partial linkage to each other, independently of their sex-linkage. Punnett,[7] in referring to the same paper, has said, "Morgan's experiments with *Drosophila* suggest coupling of some kind between factors for eye color and shape of wing, though both of these factors may show sex-limited inheritance in other families." A study of the data referred to, or of any of the similar data on *Drosophila* since published, will show that these genes *always* show sex-linkage, and that *at the same time* they always show linkage to each other when both can be followed in the analysis. The two phenomena are not mutually exclusive, but both are always present.

Both Tanaka (in a footnote) and Punnett refer to the latter's case in rabbits as the first example of linkage in animals not involving sex. If the linkage between sex-linked genes is, for some strange reason, not considered to belong in this category, there are still at least two cases which antedate Punnett's slightly. A few months before Punnett's paper appeared I had suggested[8] the possibility of linkage in mice. It now seems rather probable that the relation in both mice and rabbits may really be that of

[3] *Zeits. f. ind. Abst.-u. Vererb.-Lehre.*, VI, 1912.
[4] *Jour. Genet.*, III, 1913.
[5] *Science*, N. S., XXXVII, 1913.
[6] *Jour. Exp. Zool.*, XI, 1911.
[7] *Jour. Genet.*, II, 1912 (Nov.).
[8] AMER. NAT., XLVI, 1912 (June).

triple allelomorphism. For this reason I am inclined to assign priority to Morgan and Lynch,[9] whose paper on linkage of genes in *Drosophila* which are not sex-linked appeared after my own paper and before Punnett's.

COLUMBIA UNIVERSITY A. H. STURTEVANT

NABOURS'S BREEDING EXPERIMENTS WITH GRASSHOPPERS

IN a recent paper, Nabours ('14) describes breeding experiments that he has been carrying on for some years with grouse locusts of the genus *Paratettix*. His work is of special interest in showing that in a wild species there exists a number of distinct types that show alternative inheritance of a particular kind. His paper may be summarized as follows:

1. Nine distinct, true breeding forms of *Paratettix* were collected "in nature." These "species" (as Nabours is inclined to consider them) "are mainly distinguished by their striking color patterns."

2. When an individual of one of these species is mated to one of a different species the hybrid character of the offspring is apparent at once, in that "all the characters of each parent are represented in the F_1 hybrid." In other words, the hybrid is in a certain sense an intermediate, and "the terms dominant and recessive" are probably not "applicable at all." This point, while of little theoretic importance, has a practical value in that the zygotic constitution of any hybrid can be recognized without further breeding tests.

3. With one exception, each color pattern factor was found to behave as an allelomorph to any other color pattern factor.

4. The various lengths of the wings and pronotum are apparently not inherited, as such but are determined by environmental factors, especially such as tend to prolong or to shorten the length of larval life.

It appears that Nabours confuses the relation of the facts mentioned under 3, and that he supposes this to be the ordinary behavior of "mendelizing characters," for he says:

> The essential result of these experiments has been the extension of this principle [Mendelian inheritance] to a considerable number of types of a phylogenetically low group of ametabolous insects.

To be sure, he recognizes that other workers in genetics have an attitude quite different from his, and he takes some little pains to make clear his own point of view. To quote again (p. 142):

[9] *Biol. Bull.*, XXIII, 1912 (Aug.).

The existence of unit characters in the De Vriesian sense does not appear to have been as clearly demonstrated as that of alternative inheritance . . . and the interpretations are at great variance. Thus, one group of authors [reference made to Bateson, Doncaster, and Tower] recognize characters in organisms that can be replaced by other characters when the proper crosses are made, . . . while on the other side there are those [references to Whitman and Montgomery] who believe that the organism as a whole is the only unit and that there are no actual unit characters.

Again he says (p. 169):

No character of one parent species is ever replaced in the F_1 hybrid by any character of the other parent. All the characters of each parent are represented in the F_1 hybrid. It follows then that these grasshoppers do not exhibit characters which by crossing can be replaced by other different characters; the whole pattern appears to be the only unit.

There is no real conflict between Whitman's idea and the accounts given by students of Mendelism, for the latter realize that far-reaching somatic effects may result from a single factor, and the composite character of the hybrid is not an uncommon occurrence. Nabours identifies a particular pattern with the "organism as a whole," but since his evidence relates here to color patterns only, nothing is gained by the introduction of such a vague phrase as the "organism as a whole." Specifically he shows that the hereditary differences between any two types can be explained on the assumption of a single differential for each case.

With reference to the antithesis presented by Nabours, it must be recognized that the modern literature of Mendelian heredity affords innumerable instances where two or more characters entering from one parent and their allelomorphs from the other, reappear in the F_2 generation in new combinations.

If we assume with Nabours that each of the eight color patterns are represented by a characteristic condition of the "germinal material," we may use his terms *A, B, C, D, E, F, H* or *I* to symbolize this "germinal material" for the various color patterns. As Nabours uses the terms, an individual homozygous for *A* is represented simply by *A*, and a hybrid between *A* and *B* by *AB*. In ordinary usage, the homozygous form would be represented as *AA* and its germ cells by *A*. This is a minor matter. Ordinary usage has the advantage of being more consistent.

According to Nabours, then, *A* mated to *B* gives *AB; B* mated to *F* gives *BF; C* mated to *E* gives *CE*, etc. In gametogenesis these factors segregate, so that, for example, *BA* gives germ cells

A and *B; BF* gives *B* and *F*, etc. In other words, he treats the matter as if he were dealing with a system of multiple allelomorphs, though he nowhere specifically calls them such. From this point of view there are eight distinct allelomorphs concerned with color pattern any two of which may constitute a pair; in any zygote two allelomorphs (perhaps alike, perhaps unlike) will be present, and in any gamete only one of the eight will normally occur.

With one exception of which I will treat later, all of Nabours's results can be explained by this hypothesis. This sort of explanation is not new. (Shull ('11), de Meijere ('10), Sturtevant ('13) and others have used it to explain results obtained in *Lychnis, Papilio,* rabbits and other forms, and it will almost undoubtedly be shown to apply satisfactorily in still other cases.

The exception just mentioned occurred in the cross which Nabours describes at the bottom of page 156 (*e*). Here a male of the constitution *CE* was mated to a female of the constitution *BI*. On Nabours's theory, the gametes of the male should carry *C* or *E*, but not both, and the gametes of the female should carry *B* or *I*, but not both. The union of the two kinds of sperms with the two kinds of eggs should give four classes of offspring, and these were in fact obtained; viz., 12 *BC*, 11 *BE*, 7 *CI*, 10 *EI*. But there appeared also one individual *BEI*. Nabours's explanation of the case is that perhaps the *BI* "female parent gave at least one gamete containing the factors for the patterns of both her parents and that this double character gamete was fertilized by one of the *E* gametes which came from the *CE* male."[1] Let us see whether this is the most probable interpretation.

As Sturtevant has pointed out, for any case to which the idea of multiple allelomorphism is applicable, an equally valid explanation may be found in "complete linkage" of the factors concerned. To decide in any case between the two explanations would be impossible.

If, however, linkage were not complete, a "cross-over" class or "recombination" class might occur, and this would suffice to rule out the explanation based on multiple allelomorphs.

Such a "cross-over" class perhaps is furnished by the *BEI* individual. The demonstration of this may be given by the use of symbols, as follows:

Let us assume that *A* is the allelomorph of *a*, *B* that of *b*, *C* of *c*, *D* of *d*, *F* of *f*, *I* of *i*, etc., making eight pairs of allelomorphs altogether. Assume that each gamete of any individual carries

[1] This explanation is essentially similar to that advanced by Bridges ('13) to explain certain peculiar results in *Drosophila*. Bridges assumed that in gametogenesis the two X-chromosomes of a white-eyed female failed to segregate (in Bridge's terminology, non-disjunction occurred), and passed over together into one gamete.

one allelomorph of each pair, and that the eight factors thus present in a gamete form a linked group, tending to segregate as a unit in gametogenesis. Thus Nabours's form *A* would give gametes of the form *Abcdefhi*. *AB* would give gametes of only two forms, one corresponding to *A* and the other to *B*, viz., *Abcdefhi* and *aBcdefhi*. Two other forms are possible, formed by the exchange of *A* with *B*, and of *a* with *b*, but these will not occur if linkage is complete. In dealing with the hybrid *AB* in practise the factors *cdefhi* would not be put into the formulæ, as they are alike in all gametes.

These rules would apply similarly to all other species and hybrids. Therefore in the case in which the *BEI* individual occurred, we would represent the male parent, which Nabours designated *CE*, by *bCei–bcEi*, and its gametes by *bCei* and *bcEi*. The female parent, which Nabours designates *BI*, we would represent by *Bcei–bceI*, and its gametes would be *Bcei* and *bceI* if linkage were complete. If linkage were not complete there would occasionally be formed gametes *bcei* and *BceI*. One of these latter (*BceI*) was probably formed and fertilized by a sperm of the type *bcEi*, thus giving rise to the *BEI* individual. No gametes corresponding to *bcei* appear to have been fertilized, though of course we do not yet know what the appearance would be of an individual so formed.

This matter would be easy to test, and it is to be hoped the cross may be repeated. If then *BEI* forms should appear again and in these when mated to other forms the factors B and I should be found to stay together to the same extent as they before separated, it would show that close linkage, rather than multiple allelomorphism explains this particular instance.

It may be, too, that both linkage and multiple allelomorphism play a part in the production of these phenomena. In any case it seems that the test is at hand, and not difficult to perform, excepting in so far as there are practical difficulties connected with the rearing of the grasshoppers in sufficient numbers to cover the point.

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